

TOWARDS A DECISION-MAKING CULTURE IN WILDLIFE MANAGEMENT:  
AN INTEGRATIVE STUDY OF SCIENTIFIC DECISION SUPPORT

by

TARA GANCOS CRAWFORD

(Under the Direction of Clinton T. Moore and James Martin)

ABSTRACT

Decisions made on our behalf by managers of the public trust are inherently complex. Tradeoffs are inevitable and choices are required despite pervasive uncertainty. First, focusing narrowly on the issue of scientific uncertainty at the species population level – the micro-scale, I consider data limitations and analytical constraints that make scientific inferences about population biology and demographic processes difficult. More specifically, I developed a novel integrated population model for American alligators (*Alligator mississippiensis*) to improve agency understanding of alligator population dynamics despite multiple interacting sources of uncertainty. I then verified model behavior using simulation. Second, zooming out to consider how science informs management - the meso scale, I address technical challenges limiting direct application of available research and monitoring data in policy deliberations. In my second empirical chapter, I implemented a genetic algorithm to identify an alligator harvest policy that sets annual harvest quotas to optimize long-term management objectives based on data from existing monitoring programs. The forward-looking approach accounts for multiple sources of uncertainty and can be tailored to other species with complex life histories and different agency

contexts. Lastly, at the broadest level – the meta scale, I examined collaborative applications of structured decision making (SDM) in wildlife conservation and management through the lens of relational power. In my third and final empirical chapter, I present an autoethnography to illuminate how individual and institutional relationships shape SDM practice and its portrayal in the peer-reviewed literature. My dissertation demonstrates robust and flexible analytical tools that can help resource managers translate scientific research and monitoring data into actionable knowledge. It also speaks to the insufficiency of focusing exclusively on the technical dimensions of making science useful to managers.

INDEX WORDS: Harvest management, Tradeoffs, Uncertainty, Integrated population models, Bayesian inference, *Alligator mississippiensis*, Optimization, Approximate dynamic programming, Genetic algorithm, Integrative conservation, Relational power, Autoethnography

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## DEDICATION

For Audrey Howell, Hutch Sanders, Mike Hooker, Ashley Block, and Kate McFadden, my cherished friends and colleagues who departed too soon and whose memory offers a bittersweet reminder of the fragility of our human experience, and Woodrow, my hard lurkin' dog.

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## CHAPTER 1

In the United States, federal and state resource management agencies set the terms for many kinds of human-wildlife interactions. As public trust resources, wildlife theoretically belong to everyone and to no one. Government authorities, the trustees, acting on our behalf, decide where, when, how, and by whom actions may be taken so the benefits of wildlife resources are sustained. In doing so, fish and wildlife management agencies (agencies) shape social and ecological systems in diverse and consequential ways. Because public perceptions regarding the use, protection, or manipulation of wildlife populations vary, conservation and management decisions require tradeoffs among multiple, sometimes competing or conflicting, stakeholder objectives (Hirsch et al., 2010; Jacobson & Decker, 2006; McShane et al., 2011).

Explicit consideration of tradeoffs requires integrating information about stakeholder values with scientific understanding of the management system, specifically its current state (conditions and circumstances) and how it will change in response to proposed policies or actions. The satisfactoriness of any management strategy depends on how it will affect the things people care about compared to proposed alternatives. In our complex, uncertain, and dynamic world, the consequences of any decision cannot be predicted without error. Still, decisions must be made, or, by default, the choice is to do nothing and maintain the status quo.

With interest in helping agencies identify and evaluate wildlife conservation and management tradeoffs despite multiple sources of uncertainty, I examined how conservation researchers support decision making at multiple scales of environmental governance, which I present in Chapters 3, 4, and 5. Environmental governance – the ways and means through which

society organizes to influence natural resource policy – is bigger than any one institution or sector of society. My work primarily focuses on decision making within/by government agencies, but environmental governance emerges beyond the government, through relationships and interactions among state actors, non-government organizations, communities, and industry (Advancing Conservation in a Social Context (ACSC), 2011).

In the following chapter (Chapter 2), I lay a foundation for my dissertation research. First, I introduce complexity as a fundamental characteristic of wildlife management systems that affects what we know about the world, how past circumstances and conditions co-constructed our path to the present, and how things may change in the future based on our choices. Pertinent here, complexity necessitates consideration of tradeoffs and uncertainty in resource management decisions. Second, I give a brief history of wildlife management in the United States to clarify how conservation and management practices evolved over the last 150 years in response to accumulating knowledge and shifting social values and norms. Third, I introduce a framework for addressing complex resource management decisions, those with multiple objectives and alternative courses of action, known as structured decision making (SDM). Fourth, I explain the integrative framework for conservation research and the necessity of pluralism in any meaning-making process intended to guide conservation policies or practice. Lastly, I set the stage for the subsequent chapters, Chapters 3 and 4, by introducing the alligator harvest management decision support project that catalyzed this work.

In Chapter 3, my first empirical chapter, I focus on reducing epistemic sources of uncertainty related to American alligator (*Alligator mississippiensis*) population biology and the mechanisms responsible for population change over time and in response to management actions, specifically harvest. I evaluate an integrated population model (IPM) for alligators in

terms of its ability to overcome analytical limitations encountered by researchers in past attempts to model alligator population dynamics. Unlike modelling techniques used previously, integrated population models analyze multiple types of population data in parallel, allowing for information about population parameters available in each type of data to inform one another, while accounting for multiple sources of uncertainty. I fitted a prototype alligator IPM to replicate sets of simulated data over ten trials ( $n = 10$ ) in a Bayesian framework and examined the model's ability to recover the latent (unobserved) parameter values used to generate population time series from which the data came.

In my second empirical chapter (Chapter 4), I demonstrate a framework for identifying a harvest policy for setting annual alligator harvest quotas that optimizes long-term management objectives. Current agency approaches use statistical trend models and retrospective checks that leave agencies vulnerable to surprises. The biological modelling framework developed in Chapter 3 to simulate alligator population dynamics is linked to existing monitoring protocols (count surveys) to produce a harvest quota based on count data and understanding of how the population will respond. Using forward simulation in a genetic algorithm optimizer, I demonstrate a process for finding parameter values for a harvest policy function that maximizes long-term objectives. I show that simple stochastic modeling can be an improvement over ad-hoc trend-based analyses of population counts being used currently.

My third, and final, empirical chapter (Chapter 5) is an autoethnography of my experience developing analytical methods to facilitate science-based alligator harvest management decision making and facilitating teams of wildlife professionals addressing real-world conservation issues at structured decision making (SDM) workshops, during my doctoral program. Using examples from my lived experience, I illuminate relational power dimensions of

collaborative resource management applications of structured decision making (SDM), neglected by existing scholarship, but consequential, nonetheless.

Finally, to conclude my dissertation, I review what may be learnt from the preceding chapters and discuss how they independently and collectively contribute to our understanding of science-based decision support in wildlife conservation and management. I reflect on how the integrative principles of complexity, context, and pluralism manifested in my work, and recommend other novice integrative researchers consider autoethnography as a process for reflexivity and a product of integrative research.

## CHAPTER 2

### **Conceptual and Theoretical Framework**

From cells to societies, life manifests through interdependent systems of interconnected parts that interact and react to their environment and one another, known as complex adaptive systems (CASs) (Levin, 2002). CASs may be conceived as information structures and communication processes that produce emergent and dynamic phenomena that exhibit a tendency for self-regulation and self-direction (Buckley 1968). Recognizing wildlife conservation and management as CAS among CASs has implications for how scientists conduct research and support resource management decision making.

Human health, social justice, economic affairs, and national security shape and respond to the abundance and distribution of natural resources, and ecosystem change and resiliency (Lubchenco, 1998). Interdependencies between systems emerge from a diversity of multi-scale direct and indirect relationships among constituent parts. The systems we study and the systems through which we study them are dynamic and relational, and they exhibit non-linearities and emergent properties. It follows that the environment for decision making in the public sphere is itself complex, dynamic, and only partially knowable (Keeney, 1982).

While it may be easy to broadly classify conservation challenges (e.g., over harvest, habitat loss, disease), resource management outcomes depend on the social, ecological, and institutional factors involved in each context. For example, communal property, private property, and government property have each been demonstrated as successful and as failed property -

rights regimes in different settings (Feeny et al., 1990). The context-dependency of resource management conflicts precludes 'one size fits all' solutions.

Management outcomes, such as changes in wildlife populations, are hard to predict and may be difficult to detect when they do occur because data, models, or disciplinary theories only allow us to partially describe features (Ryder et al. 2010). Four sources of uncertainty are commonly discussed in environmental management contexts: partial observability, structural uncertainty, stochasticity, and partial controllability. Our inability to perceive ecological systems without error is a type of uncertainty known as partial observability (Ludwig et al., 1993). Sampling error, the imperfect measurement of populations or field conditions, sampling error, reduces the accuracy of monitoring and research data available to inform decision making (Williams et al., 1996). Structural uncertainty is a type of epistemic uncertainty that is produced by incomplete understanding of the nature of ecological relationships, such as the mechanisms driving population dynamics over time (Williams et al., 1996). Seemingly random, inherent variability in natural or human systems, known as stochasticity or indeterminism, arises from fluctuations in environmental conditions (e.g., precipitation and water levels) and biological factors (e.g., demographic rates) (Ascough et al., 2008). Though often confused with structural uncertainty, unlike structural uncertainty and other sources of epistemic uncertainty caused by limited scientific data or knowledge regarding how a process is modeled, stochasticity is a form of aleatory variability within a process; it cannot be reduced through additional research. Lastly, partial controllability describes agencies' inability to assert complete control over how management policies are implemented. Though partial controllability gets less attention in the literature, it affects the likelihood that a particular policy decision will produce desired outcome(s). Acknowledging the likelihood that intended management actions (e.g., hunting

quotas) and actual management implementation (e.g., total annual harvest) may differ can help managers better understand whether a particular policy decision will produce desired outcomes.

Ignoring complexity only increases the likelihood of unforeseen consequences emerging that have potential to undermine policy decisions. To better understand management options and the probability of achieving expected results despite the challenges presented by complexity, agencies need to account for their partial understanding of the systems they endeavor to manage (Kleiven et al., 2004).

### **Managing Wildlife as Public Trust Resources**

In the United States, government institutions possess regulatory authority and fiduciary responsibility for wildlife populations as public trust resources. At the time of genesis for state regulatory agencies (1860s – 1920s), rural agrarian communities, hunters, and trappers were their primary stakeholders and their mounting concerns for declining populations of game species and the role of market hunting were key drivers in their formation (Jacobson & Decker, 2006).

Driven by utilitarian values, management priorities were based on the concept of maintaining populations on/for a sustained yield basis (Jacobson & Decker, 2006; Nie, 2004; Patterson et al., 2003). The field of practice prior to the 1920s consisted of informal ethical codes that developed within hunting and sportsmen's clubs to sustain recreational hunting opportunities, primarily for ungulate species (Conover & Conover, 1997).

When animal ecology emerged as a scientific discipline in the 1920s-1930s, insights and theories about species interactions and wildlife communities were recognized for their potential to guide policy (Brulle & Benford, 2012). A discursive shift from the foregoing emphasis on protecting game species for harvest towards a discourse of wildlife management was accompanied by a cultural shift that spurred significant structural re-organization and advocacy

goals (Brulle & Benford, 2012). In the decades that followed, greater awareness of environmental issues continued shifting public perceptions, and social values for wild creatures and places expanded and diversified (Jacobson & Decker, 2006).

Society has become more heterogeneous. Traditional wildlife stakeholders (i.e., hunters, trappers, other consumptive resource users) remain key benefactors of sustainable resource management; however, they comprise a diminishing portion of constituents interested in agency conservation and management decisions (Bischof et al., 2012; Jacobson & Decker, 2006; Poudyal et al., 2008). Stakeholders today have varying opinions about agency legitimacy and sometimes view these governing bodies as “biased, exclusive, or unrepresentative of non-consumptive stakeholder values” (Jacobson & Decker, 2006; Nie, 2004). The long-term effectiveness of state management institutions depends on their ability to connect with broad societal principles and customs that legitimize them to society (Jacobson & Decker, 2006). Given the high stakes and potentially diverse audiences attendant to resource management decisions, agencies require a decision-making framework that clarifies tradeoffs among proposed policies or actions. Agencies want to mitigate the potential for undesirable outcomes, ranging from unexpected changes in resource conditions to legal disputes initiated by negatively impacted stakeholders.

Many management strategies are biologically sustainable; value-based preferences determine the optimality of alternative actions (Nichols et al., 2007). While ecological data and theory are central to developing viable management strategies and predicting their outcomes, science alone is insufficient for making good policy choices (Primm & Clark, 1996). Along with scientific data and expertise, stakeholder involvement is vital for developing effective and durable conservation policies (Decker et al., 2014). Initiatives that fail to account for human

dimensions of conservation, including variability in public attitudes regarding what is acceptable for resource conditions, tend to be less successful than anticipated (Kleiven et al., 2004; Uphoff, 1999).

Good management outcomes, those that are highly valued, cannot be guaranteed, so the quality of any decision depends on the process of deliberation that led to it. Decisions should be based on our best understanding of how alternative choices affect the things that are valued by the decision maker. Sound conservation decisions require transparency, consistency, communicability, analytical rigor, and responsiveness to stakeholders (Fuller et al., 2020). Rather than search for comprehensive synoptic solutions or default to the status quo, wildlife conservation and management needs to directly acknowledge stakeholder values and tradeoffs, along with gaps in scientific understanding, and areas of disagreement and uncertainty, then find ways to account for them in decision making (Hirsch et al., 2013).

### **Towards a Decision-Making Culture Through Structured Decision Making**

*"The problem of the decision maker is to select a course of action in a world that is perceived as uncertain, complex, and dynamic"* (Howard, 1968).

In the late 1990's, a grass-roots effort by professionals within the U.S. Geological Survey (USGS) and U.S. Fish and Wildlife Service (USFWS) began promoting structured decision making (SDM) among federal and state agencies with authority over natural resources, particularly fish and wildlife, and their habitats (Runge et al., 2013). In many cases, agency scientists noticed environmental management decisions were not constrained by a lack of information but insufficient procedures for incorporating information about decision makers' values with expert judgments of fact and data within a formal process that compares alternative courses of action (Keeney, 1982). The appropriateness of a choice is rooted in moral or value-

based orientations beyond science (Gregory et al., 2012). Conservation and management decisions are determined by human preferences, social context and relations, and ethics (Gregory et al., 2012).

Informed by behavioral decision theory, and research in psychology and economics, SDM is a “values-focused” approach to problem solving that uses procedural tactics and analytical methods to clarify tough choices affecting the things we care about. The SDM process involves iterating through five stages of problem structuring and analysis, which frame the decision opportunity, deconstruct it into its essential elements, and reconstitutes those elements into a framework that clarifies tradeoffs. The stages, summarized by the acronym ProACT, include: 1. Define the decision problem (Pr); 2. Specify objectives (O); 3. Identify alternative choices (A); 4. Forecast consequences (C) of alternatives in terms of objectives; and (5) Evaluate tradeoffs (T) associated with expected consequences. Proactively structuring decisions not only facilitates agency insights regarding the satisfactoriness of alternative management options, it clarifies sources of debate or uncertainty bearing on a difficult decision (Gregory et al., 2012, pp. 1–20).

### **Complexity and Complex Adaptive Systems**

*"When we try to pick out anything by itself, we find it hitched to everything else in the Universe."*

- *John Muir*

Despite understanding complexity as an inherent property of social-ecological systems, developing and testing complexity theories in conservation research can be difficult. Complexity theory is a conceptual departure from many disciplinary perspectives, which apply specific philosophical perspectives and methodologies to explore interactions among constituent components of the larger whole (Bennett & McGinnis, 2008). Many conservation researchers are

trained in the life sciences, but study conservation issues in systems where people – our culture, politics, economy – generate and mediate positive and negative impacts (Adams, 2007).

Conventional scientific training overlooks social aspects of conservation decision making as well as philosophical perspectives of other disciplines (McNie, 2007).

Different philosophical perspectives and epistemologies handle complexity differently, e.g., broadly speaking, realists at one end of the ontological spectrum seek universal truths about the world that exist independent of our perception of them while relativists at the other end of the spectrum seek understanding of individualized and contextualized experiences of the world (Moon & Blackman, 2014). Historically, natural scientists adhered to a realist ontology, but relativist ontologies are gaining traction. Doing conservation research and using it to inform policy requires recognizing the dynamic nature of ecosystems and their capacity for continual surprise because simplified system representations inevitably leave out system components (van Kerkhoff, 2014). Efforts to analyze sub-components of a complex system ignore other parts of the system for the sake of analytical manageability, but it does so at the cost of generating uncertainty (Ryder et al., 2010).

In complex systems, significant uncertainty in the nature and timing of impacts arising from interventions make it difficult to evaluate policy outcomes. Multiple interventions may be operating at a given time and interacting, making it hard to disentangle the outcomes of each (Walton, 2014). It can be difficult to delineate when the impacts of one intervention end and those of another begin, which complicates efforts to attribute credit for successes and failures. Further, among those present within a particular social-ecological context, perspectives also vary with regard to a problem's origin, impact, and significance (Rochefort & Cobb, 1993), and policy outcomes exhibit path dependency.

Accounting for ecological complexity in conservation research and practice requires different types of expertise and contributions from all disciplines to a shared knowledge base (Lubchenco, 1998). Narrow problem definitions framed from a single philosophical perspective ignore complexity as if it did not exist, which is insufficient to mitigate 21st-century challenges (Lubchenco, 1998). Problem statements and definitions are best developed as a team activity by people with varied but complementary knowledge (Primm & Clark, 1996). Interdisciplinary teams, as well as interdisciplinary people, are needed to overcome the difficulties inherent in translating among different ways of knowing, to think differently and create a better understanding of our work (Adams, 2007).

There are many ways to experience, describe, and understand resource management issues. Many perspectives are valid, none are complete. Different epistemological perspectives frame problems around different axes of inquiry that are inherently partial descriptors of the world. Working across disciplines to develop useful constructs of socio-ecological complexity will require a common understanding of how different actors construct new knowledge (Pahl-Wostl, 2002).

### **Integrative Conservation Research**

Diagnosing complexity helps to ensure conservation science is not limited to positivist-oriented disciplines that conduct research characterized by principles of objectivity and rationality that seeks a mechanistic understanding of causal relationships among parts of the system (Mendoza & Martins, 2006; Mendoza & Prabhu, 2002; Roebuck & Phifer, 1999). Claims that a decision is “scientific” are intended to imply a special kind of merit or reliability, suggesting the claims are well-founded and perhaps beyond dispute (Chalmers, 1999). Purely objective evaluations of socio-ecological problems and solutions are impossible. Our

professional values and norms dictate how evidence is interpreted and shape our perspective on how study results should be understood and used, and how valid or useful they are (Ryder et al., 2010). Though scientists may strive for objectivity in their research, it is impossible to disengage from the social context of knowledge work, which is structured by power disparities.

My PhD program, the Integrative Conservation PhD program (ICON) at the University of Georgia (UGA), strives to illuminate and account for tradeoffs inherent to complex socio-ecological issues to better understand what is lost and what is gained by different policies or practices. A key part of the ICON curriculum is pluralism - engaging multiple epistemologies and methods in research. Different philosophical framings allow integrative researchers opportunities to explore the interface between different perspectives to better know the status of resources, array of decision-making arrangements, and interactions between regulators and resource users (Hirsch et al., 2013; van Kerkhoff, 2014). A plurality of approaches counters the trend towards positivism in conservation research.

Considering conservation issues and interventions through different analytical viewpoints provides a more comprehensive understanding of problems and proposed solutions, and reveals the importance of actors, institutions, and their relations in, and in relation to, decision problems (Hirsch et al., 2013). Early in the program, students engage different philosophical perspectives related to knowledge and its role in environmental governance. Perspectives provided by different epistemologies regarding the importance of actors, institutions, and their relations in, and in relation to, decision problems provide a more nuanced understanding of the context in which particular sources of uncertainty are appreciated, and how actions taken to address uncertainty interplay with other possible framings of what makes conservation decisions hard.

Conservation researchers' assessments of conservation issues are only one of many equally valuable ways of understanding of complex systems (Turkle & Papert, 1990).

Pluralism acknowledges interdependencies in socio-ecological systems (Roebuck & Phifer, 1999), including the biases researchers, such as myself, carry into our work, which need to be acknowledged. Personal and epistemological biases cannot be treated as independent from the way we engage in conservation and research because our philosophical perspective and disciplinary norms and values guide our science, teaching, and service pursuits. Throughout the scientific process evaluative judgements are made based on researchers' perspectives regarding what constitutes important, relevant, and urgent research (Roebuck & Phifer, 1999).

Students in the ICON program are expected to, as integrative conservation researchers, practice reflexivity – an ongoing practice of self-reflection; identifying how our identities and limitations as individuals impact our work, and recognizing how the research process itself changes us in return (Moon & Blackman, 2014). Reflexivity is an important, recognized component of qualitative research that helps ensure professional integrity and rigor. Some argue personal and methodological reflexivity is essential to the validity of qualitative and quantitative research of all kinds (Finlay, 1998).

As a PhD student working at the interface of science and policy, I am both a knowledge generator and consumer. Outside of the university I relate to other conservation professionals as both participant and observer. In applied research settings, researchers are agents within the study system, directly engaging the subject. In the case that we work collaboratively on an intervention that is applied or adopted by our collaborators, we are not objective observers. This may be consequential for our contributions and the subjectivities they produce. The nature of

environmental governance as a complex adaptive system means our work within the system inevitably changes the system itself as our relations respond to our presence.

### **Alligator Harvest Management Programs**

A prime example of the challenges inherent to multi-objective wildlife management decision making, I use American alligator (*Alligator mississippiensis*) harvest management programs as a model system for putting concepts such as tradeoffs and uncertainty in context and studying science-based decision support tools. My work with alligator managers began in fall of 2013. My advisor and I held a series of meetings with state wildlife agency professionals responsible for alligator harvest programs in the species' eastern range, who I will refer to as "managers." We made one to two-day trips to visit agency representatives in Georgia and neighboring states to conduct "listening sessions." Our wide-ranging discussions during these meetings were facilitated by a questionnaire that we distributed prior to the meeting. The questionnaire-guided discussion focused on things, products, and policies encountered by alligator harvest managers in their professional roles, not on managers' personal thoughts, perceptions, feelings, or ideas. We asked managers open-ended questions about the structure of their state's alligator management program(s), explicit and implicit objectives for public alligator hunts, management actions or policies used or in consideration, method of choosing an alternative when setting regulations, alligator monitoring program design, critical uncertainties that make decision making challenging, and areas of dissatisfaction or concern with their program (Appendix A).

A review of agency documents and websites complemented the information gleaned from our meeting with each agency, and we identified common and distinctive elements of alligator harvest management and decision-making challenges across institutional contexts. In December

2013 and December 2014, we convened multi-agency decision-structuring workshops with our collaborators from across the species' eastern range to synthesize and discuss our findings. We concluded that public alligator harvest program management stands to benefit from development of a SDM framework that directly links scientific data and expertise with information about stakeholder values in evaluations of harvest policy options, accounts for multiple sources of uncertainty, and facilitates consistency, transparency, and analytical rigor.

Managers want to mitigate the potential for undesirable management outcomes to emerge, ranging from unexpected changes in resource conditions to the initiation of legal disputes by negatively impacted stakeholder groups. For harvested species and large carnivore species, a defensible decision framework is particularly necessary. Resource management, particularly population control, is not always achieved in the manner anticipated (Bischof et al., 2012), which contributes to the debate of recreational hunting as an appropriate means of wildlife management. We found that identifying optimal policies based on species biology and principles of resource sustainability requires analytical methods not yet used by many state agencies. Despite widespread agreement regarding the need to base conservation and management decisions on available science, agency decisions are commonly based on managers' intuition, informed by their scientific training and years of experience (Runge et al., 2013). This determination motivated the analytical work presented in my first two empirical chapters, Chapters 3 and 4.

In summary, complexity is an immutable feature of social and ecological systems, which cannot be ignored in environmental decision making. Diverse public perspectives regarding the value of wildlife populations means conservation and management decisions typically involve multiple objectives, which obligate tradeoffs. Identifying and evaluating tradeoffs requires

integrating information about how managed systems generate consequences for stakeholders and how stakeholders value those consequences. Our capacity to predict management outcomes without error is limited by interacting sources of uncertainty: partial observability, structural uncertainty, indeterminism (stochasticity), and partial controllability. Any method for making sense of uncertain information (data) produces an incomplete understanding of complex adaptive ecosystems. Since the early days of wildlife management, more than a century ago, ecological systems and their relationships with social systems have changed, along with expectations for how they are managed. New approaches to research and governance are appropriate. For conservation researchers, pluralism provides integrative insights about natural resources and their governance that transcend the narrow sightedness of any single disciplinary perspective. In governance spaces, structured decision-making approaches are promoted as means to integrate contributions from policymakers, scientists, and stakeholders in a process that disentangles subjective preferences and technical judgements while recognizing the important and unique contributions of each in identifying acceptable tradeoffs among coexisting objectives (Gregory & Keeney, 2002).

## CHAPTER 3

### **Modeling Alligator Population Dynamics Using an Integrated Population Model: Evaluating a Prototype Using Simulation**

The American alligator (*Alligator mississippiensis*), hereafter alligator, is among the most studied crocodylian species in the world. Since population declines spurred legal protections across the southeastern United States in the 1970s, research scientists and agency biologists have been focused on improving our understanding of alligator population dynamics. Despite long-term investments in research and monitoring, scientific uncertainty associated with the biological drivers of population change remains an impediment to science-based management decisions.

In wildlife management contexts, management forecasts produced by predictive population models provide a basis for evaluating policy options and making comparisons among alternatives according to how well they achieve population management objectives. When integrated with information about value-based preferences for predicted consequences, population models help illuminate tradeoffs associated with different decision options and a preferred alternative may be identified (Williams & Johnson, 2013). To be capable of providing unambiguous direction for policy decisions, population models require an understanding of population processes, reliable estimates of population parameters, and information about population size and structure through time.

As a semi-aquatic, long-lived species, the alligator is difficult to study, and conventional statistical methods have been incapable of accounting for the complexity of alligator population structure and life history characteristics, including size-based life stages, delayed maturity, and

irregular reproductive cycles. For reasons I elaborate on in the Background section that follows in this chapter, past attempts to estimate alligator demographic rates (e.g., survival) and model population dynamics provided unreliable inferences about population biology and responses to harvest.

Today, integrated population models (IPMs) present alligator managers with new opportunities to translate population data into scientific understanding of alligator population dynamics, habitat use, and responses to conservation or management actions (Schaub & Abadi, 2011). IPMs analyze different types of population data concurrently within a unified biologically based modeling framework that can account for multiple sources of uncertainty and, pertinent here, can improve parameter estimation (i.e., more precise estimates, or with finer resolution). Given the relative abundance of alligator population data available in some places, IPMs may help managers resolve long-standing questions about population processes using existing data.

To determine whether an IPM framework can improve agency understanding of alligator population dynamics using existing science (i.e., agency data and published research), I developed an IPM for alligators and conducted a simulation study to verify the model's behavior. This work involved four objectives:

1. Program an alligator population simulation model to create a self-sustaining population using current scientific understanding of species biology from which replicate sets of data can be generated.
2. Simulate replicate IPM data sets to resemble alligator population count data, harvest data, nesting data, and mark-recapture-recovery data.
3. Develop an alligator IPM prototype to estimate population parameter values based on multiple types of alligator population data.

4. Verify population parameter estimates produced by the alligator IPM prototype over multiple trials, each fitting the model to a replicate set of simulated IPM data.

Before describing my methods, I provide additional context for the work in this chapter, in the Background section that follows. First, I describe the evolution of alligator management in the US. Second, I describe the species' unique ecology and life history characteristics. Third, I explain how past attempts to model alligator population dynamics fell short. Lastly, I present hierarchical Bayesian state-space models, a class of models that includes IPMs, to clarify their advantages and suitability for alligators and other cryptic species with complex ecologies.

## **Background**

### ***Alligator Management History***

Alligators are large (180 – 500 cm total length, TL, from tip of the snout to the tip of the tail) semi-aquatic crocodylians endemic to freshwater habitats (rivers, lakes, and wetlands) across the southern coastal plains in the United States, from Texas to North Carolina, and in Arkansas and Oklahoma (Conant & Collins, 1998, pp. 143–144). Though once abundant across its range, alligators were widely considered at risk of extinction in the 1970s when nearly a century of unregulated harvesting to supply commercial markets with hides coincided with accelerating habitat loss from urban development around growing human population centers (Elsley & Woodward, 2010). Alligators were among the first species classified at the federal level as endangered under the Endangered Species Preservation Act of 1966 (32 FR 4001, March 11, 1967). Federal protections were later transferred to the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 et seq. (Act, ESA)). Notably, alligators were also one of the first to be down listed. In 1987, alligators were reclassified range wide as Threatened Due to Similarity of Appearance to endangered crocodylians (Endangered Species Act, 1987). Habitat restoration

efforts coupled with a range-wide hunting moratorium were credited with helping the species recover.

In the decades that followed, alligator management objectives expanded beyond species persistence. As alligator populations rebounded and encounters with people became more frequent, agencies established nuisance alligator control programs to minimize negative interactions and assuage the public's growing concern for human safety. As time passed, expanding alligator populations inspired additional management initiatives. In some states, agencies began allowing harvest on private lands or limited egg and hatchling collection to supply commercial alligator farming operations. Many agencies eventually created public harvest programs to provide the constituents with a novel recreational opportunity while incentivizing species conservation. Today (2023), recreational alligator hunting is allowed in Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, and Texas.

### ***Alligator Ecology***

Alligators are long-lived ectotherms that defy simple classification based on their biology, ecology, or life history characteristics. Populations are size-structured. That is, life stages depend on size; species physiology, ecological interactions, and management interests vary over the course of an individual's life as it grows. Though they are considered generalist predators, alligators' diet shifts over the course of their lives as ontogenetic changes in body size, dental form, and bite force capabilities alter habitat uses and access to prey (Gignac & Erickson, 2015; Hedrick et al., 2021). As hatchlings, alligators are insectivorous. As they grow, they transition to piscivory, and their primarily invertebrate diet is slowly replaced by more and larger vertebrates. By the time they are full grown, they are opportunistic carnivores that may eat anything that can fit in their mouth.

By the adult life stage ( $\geq 183$  cm TL), alligators are sexually dimorphic. Males and females grow at similar rates during first six years of life. Growth rates slow and diverge between sexes as they reach sexual maturity with males growing faster and reaching larger terminal sizes, up to 450 cm TL, and growth ceases around 43 years of age (Lance, 2003; Wilkinson et al., 2016). Females, in contrast, reach maximum sizes less than 300 cm TL, although larger females have been documented, and growth ceases around age 31 years (Deem et al., 2021; Elsey & Woodward, 2010; Wilkinson et al., 2016).

Habitat quality influences alligator size and growth rates with regional differences in habitat characteristics driving variation in alligator population ecology across the species' range. Temperature is a key determinant of the animal's maximum size (Lance, 2003). Climatic conditions experienced by an alligator dictate the length of its growing season, i.e., the number of days that are warm enough for them to metabolize their prey and acquire mass (Lance, 2003). However, alligator body condition also depends on ecosystem productivity. For example, though warm, in the food-limited Everglades, alligators are often in poorer condition than in habitats farther north that are more productive (Lance, 2003). Everglades alligators also tend to reach sexually maturity at smaller sizes and lay smaller clutches than alligators in Louisiana (Lance, 2003).

Alligator size and sexual maturity are interrelated (Lance, 2003). Female alligators  $\geq 180.5$  cm TL are considered reproductive-size (i.e., they have reproductive potential) but minimum TL for reproductive-size females varies among populations (Woodward et al., 1992). During an experimental harvest conducted in Florida in the 1980s, which is described in more detail at the beginning of the Alligator Population Models section, below, population-level differences in the average size of females at maturity were associated with growth rate such that

lakes with faster growing alligators reached sexual maturity at larger sizes, leading researchers to conclude that the onset of maturity may be partly influenced by age too (Woodward et al., 1992). Uncertainty associated with the interrelationships between growth and sexual maturity, and the timing and drivers of reproduction are sources of structural uncertainty. Structural uncertainty is a type of epistemic, or scientific, uncertainty that manifests in our incomplete understanding of the nature of ecological relationships, such as the biological mechanisms driving population dynamics over time (Williams et al., 1996). Structural uncertainty related to alligator reproduction is one of several sources of structural uncertainty impinging on the development of alligator population models managers may use to evaluate proposed management actions (Lance, 2003).

Alligators typically begin courting in April and breed between late May and early June. From early June to mid-July fertilized females lay a single clutch of 30 to 50 eggs, buried in a mound of vegetation. The eggs incubate for roughly 65 days and in late August or early September, hatchlings approximately 23 – 26 cm in TL are liberated from the nest by the female. Less than half of sexually mature females (> 180 cm TL) reproduce in a given year and the interval between nesting events in the wild is unknown but thought to be two to four years (Woodward et al., 1992). Past research suggests no relationship between mature female size and her probability of nesting nor clutch size (Woodward et al., 1992).

Due to historic declines in alligator populations from unregulated hunting, agencies are cognizant of the potential for some populations to be susceptible to overharvest. The effects of overexploitation could be concealed by natural variability in population dynamics (often referred to as environmental stochasticity) or by changes in detectability associated with monitoring methods, known as partial observability. When harvest exceeds a biologically sustainable level

and is not detected, it can lead to population declines that are difficult to arrest and reverse (Ludwig et al., 1993).

### ***Alligator Population Models***

Forty years ago, the Florida Fish and Wildlife Conservation Commission (FFWCC) began studying American alligator populations to better understand population responses to management actions. Along with studies designed to answer basic scientific questions about species biology and life history traits, the agency established long-term monitoring programs to provide a scientific basis for conservation and management decisions, particularly with regard to harvest. Before initiating its statewide recreational alligator harvest program in 1988, the FFWCC, formerly the Florida Game and Fresh Water Fish Commission, conducted an experimental harvest of alligators  $\geq 122$  cm total length (TL) on five wetlands in the St. Johns River watershed in north-central Florida (Woodward et al., 1992). The objectives of the harvest study were to: (1) determine the effects of a sustained commercial harvest on alligator populations; (2) improve the accuracy of estimates for basic alligator population demographic parameters, and (3) develop guidelines for administering hunts.

Prior to the experimental harvest, population responses to alternative harvest policies were forecasted using survival and transition rates from static life table-type analysis under the assumptions of a stable size distribution and constant environmental effects (Nichols et al., 1976; Rice & Percival, 1995). Maximum sustained yield (MSY) theory to the data available at the time, agency biologists hypothesized that a 7% both-sex harvest could be sustained. To expedite learning, i.e., to have the best chance of observing harvest effects, they doubled that so that their intended harvest rate target for treatment lakes was 15% (Woodward et al., 1992).

Monitoring and research data collected during the experimental harvest suggested demographic mechanisms compensated for losses incurred by a sustained mean annual proportional harvest rate of 13% (Woodward et al., 1992). By the beginning of each hunting season, the density of alligators in subadult ([122, 183) cm TL), adult ([183, 274) cm TL), and bull ( $\geq 274$  cm TL) size classes appeared recovered. Annual nightlight count densities of harvestable size classes (i.e.,  $\geq 122$  cm TL; subadult<sup>+</sup>) were stable or increased over time, but there was a 45% reduction in counts of adult<sup>+</sup> alligators ( $\geq 183$  cm TL) (Woodward et al., 1992). The magnitude of the decline in adult<sup>+</sup> counts and a similar trend in median TL of hunter harvests were attributed to increased wariness among larger alligators. Abundance of juveniles ([30, 122) cm TL) increased over the same period leading to the conclusion that compensation for harvest losses occurred through increased recruitment of alligators into the smallest of the harvestable size classes, subadult (Woodward et al., 1992). Although juveniles were not harvested, the observed trends suggested the population responded to harvest by way of greater juvenile survival or production. It reasons that an increase in physical (TL) growth rate could lead to hatchlings becoming juveniles more quickly, but the experimental harvest researchers found no evidence of a change in the rate of individuals' TL growth (Woodward et al., 1992).

Despite removal of adult females from the population through harvest, annual nest counts were stable or increasing. The proportion of mature females in the population that were postpartum (i.e., that nested) and clutch sizes remained stable. There was no evidence of females nesting more frequently (e.g., from once every couple of years to nesting in consecutive years) and the minimum size of females at sexual maturity appeared stable over time (Woodward et al., 1992).

Although the FFWCC concluded that 13% proportional harvest rate of subadult<sup>+</sup> alligators was sustainable, variability in population responses to harvest among treatment lakes raised concerns that harvest rates were unsustainable in some cases. Perhaps, inappropriate quota levels were derived from inaccurate abundance estimates, or differing population dynamics produced variation among populations in their capacity to sustain harvest (Woodward & Linda, 1993). Seeking to maximize sustainable harvest rates while minimizing the probability of a population decline for alligator management units (AMUs), the FFWCC contracted Rice and Percival (1995) to develop an improved alligator harvest model using data collected during the experimental harvest study (Woodward, 1996a).

In their work, Rice and Percival (1995) investigated how demographic rates affected population responses to different harvest strategies (Woodward, 1996a). Size-class distributions and rates of transition through size classes were estimated from experimental harvest data to produce survivorship estimates for juveniles, subadults, adult males, adult females, and bulls (Woodward, 1996a). Initial simulations for the alligator population at Orange Lake (OL), which were used to examine the model's behavior and conduct sensitivity analyses, performed as expected and led to the tentative conclusion it sufficiently represented alligator population dynamics. However, forecasts produced with demographic data from other populations were unreasonable, particularly estimates for juvenile survival. Juvenile survivorship also had the greatest effect on changes in population size. Population dynamics were impacted by uncertainty in transition periods for juveniles and subadults. Sensitivity analyses suggested less than a 10% change in the survival rate for juveniles, subadults, or adult females could cause total population size to decline by 50%. Because the assumption of a stable size distribution was likely violated, estimating survival rates for non-hatchling size classes was "problematic." Notably, age

distributions were temporally variable and hatchling production was not constant (Woodward, 1996a).

Alligator management units could not be reliably grouped into biological risk categories due to parametric uncertainty associated with survival estimates derived from alligator size distribution data (Woodward, 1996a). Consequently, the results of harvest simulations generated by their model were unreliable, and Rice and Percival (1995) limited their inferences to comparing relative effects of harvest on different subpopulations instead of estimating population abundances (Rice & Percival, 1995). In the end, they concluded population forecasts were unlikely to improve without accurate survival rates, density-dependent survivorship functions, and size-specific adult female fecundity incorporated into the model (Woodward, 1996a).

A notable shortcoming of past alligator population models was their inability to account for multiple sources of uncertainty inherent to alligator populations and analyses based on different types of population data. Neither environmental nor demographic stochasticity were included in their model (Rice & Percival, 1995). Understanding the nature of the uncertainty involved in population analyses is essential because different types of uncertainty vary in terms of how they affect population inferences and their use in decision making (Ascough et al., 2008; Kleiven et al., 2004). The type of variability, or source of uncertainty, determines whether it propagates forward in time, whether it is reducible, and how it is represented in models. Methods for reducing and accounting for uncertainty differ depending on its source (Nichols et al., 2007; Tyre & Michaels, 2011). While statistical or probabilistic techniques can address some forms, others require facilitated dialogue and deliberation to resolve (Regan et al., 2002). Conservation

policies can be developed without complete or perfect knowledge, but they require explicit treatment of uncertainty (Ludwig et al., 1993).

### *Integrated Population Models*

For complex systems, hierarchical Bayesian (hB) models allow analysts to fully exploit available data and expertise while accounting for unknowns (Clark et al., 2005). Unknown variables, which in a Bayesian context include population parameters, “borrow strength” through their relationships with known values. Structured hierarchically, variables in hB models can share information, which makes parameters estimable even where data are missing. This means, despite incomplete biological information, inferences are possible for simple processes.

State-space models (SSMs), which are hB, explicitly relate imperfect observations of a system to the latent system states that are of real interest. Variation in data arising from study design or sampling errors made during data collection are accounted for separately from variation emerging from demographic stochasticity or other forms of ecological variability that can affect the system of interest. Distinguishing among sources of variation allows for inferences about the true population based on imperfect observations in the form of research and monitoring data (Kéry & Schaub, 2012; pp. 115–132). Additionally, the biological structure specified within the hB SSMs moderates widely fluctuating count data that on their own may appear to indicate a sudden population surge or decline, helping researchers to correctly interpret underlying population trends. Further, unlike traditional modeling approaches that require specialized training for each class of models and test statistics, hB models can be adapted to address a wide range of analytical problems.

Early alligator population models were constrained to deterministic processes, simplified to ignore effects that were unmeasurable due to a lack of data because complex deterministic

models require observations for all influences to run (Clark et al., 2005). For this reason, stochastic components of early alligator models were unmanageable. The ability to use stochasticity to model unknowns and unmeasurables (unobservable variables) is part of the appeal of hB models. Further, in a hB framework, both estimation and prediction (through the inclusion of future time points) are possible. With a conventional approach, estimation and prediction are addressed in separate steps and estimation uncertainty is difficult, if possible, to propagate into predictions.

In this chapter, I evaluate a particular type of hierarchical state-space models, the integrated population models (IPMs), that effectively addresses limitations of frequentist or maximum likelihood-based population models (Schaub & Abadi, 2011). IPMs analyze different types of data concurrently, within a unified modeling framework. As a type of state-space model with a hierarchical structure, IPMs allow for estimating Markovian processes, e.g., changes in a population over successive time steps based on the population at the previous time step, which are hidden (latent) due to imperfect observation (Kéry & Schaub, 2012, pp. 347–381).

SSMs differentiate uncertainties inherent to system processes from those associated with observation processes. A state process model is specified to describe the relationship between demography and population size, and an observation process model connects data to latent demographic parameters of interest, e.g., count data are described as partial observations of abundance. With the inclusion of additional models (sub-models) specifically relating other sets of demographic data to demographic parameters, the population model becomes “integrated.” Population parameter estimates emerge by exploiting partial information about underlying demographic processes governing population change over time contained in each data set (Schaub & Kéry, 2012). Within the statistical model, the likelihoods (generating distributions) of

individual datasets are multiplied together to produce a joint likelihood containing parameters in multiple different sub-model components. Inferences are made from this joint likelihood. Additionally, due to their capacity to differentiate among sources of uncertainty acting upon model outputs, IPMs can also help focus monitoring efforts toward decision-relevant data in management contexts (Kéry & Schaub, 2012; Newman et al., 2014, pp. 169–195).

## **Methods**

### ***Alligator Population at Orange Lake, Florida (1981-1990)***

For the work in this chapter, I developed an alligator population simulation model representing the alligator population at the Orange Lake (OL) alligator management unit (AMU) in Florida (FL) during the FFWCC's experimental harvest (1981 – 1990). OL was one of three treatment lakes where alligators  $\geq 122$  cm TL were subject to harvest. Located in Alachua County in north-central Florida, Orange Lake is considered eutrophic with high nutrient levels (Canfield, 1981; Woodward et al., 1992). Major habitat types within the study included 2788 ha open water, 2,150 ha emergent vegetation, 30 ha wooded swamp, and 286 ha spadderdock (*Nuphar luteum*) for a total of 5,254 ha of alligator habitat (Woodward et al., 1992). Rainfall patterns and water levels at OL include a wet period from June to August followed by a dry period from October to December. Substantial water level fluctuations occurred over the course of the harvest study, including droughts in 1981 and 1990, and flooding conditions in 1982 and 1988.

Over the course of the experimental harvest, on average, an estimated 13.5% of the harvestable population at OL was harvested each year. The average annual quota was 283 with an average total annual take of 236 alligators (Woodward et al., 1992). This was equal to an 83.4% hunter success rate, which was slightly less than the 87.5% average hunter success rate

calculated for the study overall. The average size-class distribution of harvested alligators was 50.8% in subadult, 36.5% in adult, and 12.7% in bull) size classes (Woodward et al., 1992).

Several types of alligator population and harvest data were collected contemporaneously during the experimental harvest. In terms of the data agencies may have available to fit an IPM, it provided a best-case scenario. OL experimental harvest data sets included size-structured population count data from nighttime spotlight eye-shine surveys, data from nesting and clutch success studies, and hunter harvest data. The FFWCC initiated mark-recapture studies in 1975 that continued at irregular intervals throughout the harvest study until 1991. They generated individual encounter histories for alligators that were captured, marked and released, then later recaptured alive or recovered dead through hunter harvest (Woodward et al., 1987). As a precursor to fitting an IPM to real data, I simulated data to represent the data sets from the OL alligator population during the experimental harvest. Simulating the data allowed me to validate model estimates for important population parameters, and to do so multiple times over replicate trials. Except where noted, I programmed the population system state processes and data generating observation processes based on previous alligator research conducted at Orange Lake.

The analysis presented in this chapter involved four stages (Figure 3.1). First, I developed a population simulation model describing system processes (i.e., demographic processes responsible for individual and population state changes over time). The model produced time series records, specifically individuals' life history records and population-level state summaries. Second, based on the time series records from the population simulation model, I generated IPM data sets containing different types of demographic data simulated with four data type-specific observation processes. Third, IPM data sets were fitted with the IPM using Bayesian inference. Fourth, model parameter estimates were compared to the latent, or generating, values specified *a*

*priori* or realized during the latent population and data simulation process models to determine whether the model was behaving as expected. The details of each stage are presented in the methods sections that follow, and a list of special terms defined in the Population Simulation, Data Simulation, and Estimation Model sections is provided in Table 3.10.

### ***Population Simulation***

The population simulation model generates life histories for individual alligator population members ( $i$ ) by iterating through a series of state processes, also referred to as system or demographic processes, over discrete annual time steps,  $t$ , for a total of  $T$  years ( $t = 1, 2, \dots, t_{HO}, t_{HO}+1, t_{HO}+2, \dots, T$ ). I waited until  $t_{HO}$  to initiate harvest because population size and size-class distribution vary widely over the first few decades of the simulation model before stabilizing. Harvest begins once the effects of the model's starting conditions subside.

In chronological order, annual cycle processes include: (1) hunting season harvest mortality ( $t \geq t_{HO}$ ); (2) annual survival in the absence of hunting; (3) summer reproduction that spans puberty, nesting, and hatching; and finally (4) growth that increases surviving population members' TL that transitions some individuals to the next larger size class beginning in fall  $t + 1$  (Figure 3.2 and Figure 3.3). The next year ( $t + 1$ ) commences after surviving population members from  $t$  finish growth and newly emerged hatchlings from summer reproduction in  $t$  recruit into the population. The simulated population is closed to immigration and emigration.

While alive, simulated population members were classified into one of five live states that correspond to total length (TL, cm) based size classes,  $c$ . Based on life history attributes, size classes (i.e., latent states,  $z$ ) included: hatchlings, juveniles, subadults that are large enough for harvest but not sexually mature, adults responsible for reproduction, and very large, primarily male, bulls (Table 3.1, Figure 3.2). Demographic rates varied by size class (Table 3.2).

Conditional on survival, individuals grow through an increase in their total length,  $TL_{i,t}$ , using a sex-specific alligator growth model (Table 3.3) (Wilkinson et al., 2016). As  $TL_{i,t}$  increases, individuals advance size classes. This means, in the population simulation model, the adult size class ( $c = 4$ ) contains individuals  $\geq 183$  cm TL, some of which are not yet sexually mature. For females, reaching the adult size class means having the potential to reproduce. In the years following the onset of harvest ( $t = t_{H0}$ ), subadult size and larger alligators (subadult<sup>+</sup>,  $\geq 122$  cm TL) are subject to a harvest mortality process (hunting season) at the beginning of the annual cycle. The seasonal timing of the simulated harvest corresponds to recreational alligator hunting seasons in the eastern portion of the species' range, which typically occur between August and October, after hatchlings emerge from nests. I elaborate on each of the demographic processes, below.

**Initial Population.** The number of individuals in each size class  $c$  ( $N_{0c}$ ) at the beginning of the simulation ( $t = 1$ ) equaled the estimated size class abundances for the Orange Lake alligator population between 1981 – 1987 (Delany et al., 2011) (Table 3.1). Each individual's size at the beginning of the simulation ( $TL_{i,1}$ ) was drawn from a uniform distribution with minimum and maximum values delineating typical alligator life stages (Table 3.1) (Woodward et al., 1992). Individuals' sex ( $sex_i$ , 1 = female, 2 = male) were drawn from a binomial distribution with the probability of being female based on the estimated proportion of females in each size class ( $\rho_{Fc}$ ) at Orange Lake (Table 3.1). Size class TL (cm) ranges, initial size class abundances ( $N_{0c}$ ), and the expected proportion of females in each size class of the founder population ( $\rho_{Fc}$ ) are provided in Table 3.1.

**Survival.** I modeled annual survival outside of the hunting season as a binomial process with temporally variable annual size class-specific survival probabilities,  $\phi_{c,t}$ . In addition to

stochasticity introduced through the binomial process model, survival probabilities varied from year to year due to density-dependent relationships between  $\phi_{c,t}$  and the adult<sup>+</sup> population. More specifically, survival probabilities were inversely related to adult<sup>+</sup> population density ( $D_{ad^+}$ ), which was computed by dividing the number of adult<sup>+</sup> alligators ( $N_{ad^+}$ ) by the area of Orange Lake ( $A_{OL}$ ). I used 5251.5 ha for  $A_{OL}$  throughout the simulation based on the habitat area reported in Woodward (1996a), 12,982 acres. I treated  $A_{OL}$  as constant, but alligator habitat area fluctuates with water level within and across years at OL.

Density-dependent survival is one way alligator populations may compensate for losses from harvest mortality (Figure 3.4). Years before hunting is introduced ( $t < t_{H0}$ ),  $\phi_{c,t}$  is computed in the fall from  $N_{ad^+,t,fall}$ . Thereafter,  $t \geq t_{H0}$ , hunting season (i.e., harvest mortality) precedes the annual survival process so  $\phi_{c,t}$  is computed from  $N_{ad^+,t,postH}$ ; equivalent to  $N_{ad^+,t,fall}$  less losses from harvest,  $H_{ad^+,t}$ . I assumed harvest mortality was the only source of mortality during hunting season. The annual survival process for the remainder of the year, after hunting season (here forward referred to as annual survival), accounts for all non-harvest sources of mortality. Annual survival probabilities ( $\phi_{c,t}$ ) were computed on the logit scale as follows (Figure 3.4):

$$D_{ad^+,t,postH} = N_{ad^+,t,postH} / A_{OL}$$

$$\text{logit}(\phi_{c,t}) = \text{logit}(\phi_{0c}) + b_c (\log_{10}(D_{ad^+,t,postH}) - \log_{10}(D_0))$$

Values for the size class-specific slope parameter,  $b_c$ , were derived from a simple relationship between two hypothesized survival rates at two densities: ( $D_{min}, \phi_{c,max}$ ) and ( $D_{max}, \phi_{c,min}$ ). The first point corresponded to annual survival probability for size class  $c$  when  $D_{ad^+}$  is low and the second point described survival probability when  $D_{ad^+}$  is high. Both were specified on the  $\log_{10}$  scale as deviations from an intermediate density,  $D_0$ , to prevent computational issues if density values became extreme in either direction. I set  $D_0$  equal to 0.193 ad<sup>+</sup> alligators/ha,

which corresponds to the median adult<sup>+</sup> population size estimate for OL during the experimental harvest (1981 – 1990) based on count survey data (Woodward et al., 1992). Adult<sup>+</sup> abundance estimates ranged from 514.3 in August 1990 to 1513.4 adult<sup>+</sup> alligators in September 1981 (Woodward et al., 1992). As densities, these equal 0.098 ad<sup>+</sup> alligators/ha ( $D_{min}$ ) and 0.288 ad<sup>+</sup> alligators/ha ( $D_{max}$ ). Expressing each as a deviation from  $D_0$  on the  $\log_{10}$  scale yields -0.2943312 and 0.173852 ad<sup>+</sup> alligators/ha, respectively. These values,  $(\log_{10}(\frac{D_{min}}{D_0}), \log_{10}(\frac{D_{max}}{D_0}))$ , delimited the range of adult<sup>+</sup> population densities over which size class-specific survival probabilities varied. The difference between the two, 0.4681664, became the denominator for the slope parameter  $b_c$  relating changes in  $\phi_{c,t}$  to  $D_{ad^+,t}$  in the population simulation model.

Size class-specific numerator values for  $b_c$  were computed by assuming when  $D_{ad^+,t}$  equals  $D_0$ ,  $\phi_{c,t}$  equals  $\phi_{0c}$ . Over the range of  $D_{ad^+}$  delimited above, size class-specific survival probabilities could vary above and below  $\phi_{0c}$  on the logit scale by some amount ( $\Delta\phi_c$ ), delimited by the range  $(\phi_{c,min}, \phi_{c,max})$ , which I expressed as deviations  $\phi_{0c}$  on the logit scale in the numerator for  $b_c$  (Table 3.2).

Due to differences in the ecological mechanisms underlying compensatory survival responses of different size classes to harvest,  $\Delta\phi$  varied by size class (Table 3.2). Up to approximately 91 cm TL, hatchling and juvenile alligators are susceptible to cannibalism (Delany et al., 2011). Approximately 6 – 7% of the juvenile population is lost annually to cannibalism (Delany et al., 2011). As alligators grow, they are less likely to be consumed by larger alligators, so I allowed  $\phi_J$  to vary 0.06 in either direction around  $\phi_{0J}$  and allowed  $\phi_H$  to fluctuate by 0.08 in either direction around  $\phi_{0H}$ . For subadult<sup>+</sup> alligators, I assumed changes in  $D_{ad^+}$  could result in up to a 10% change in annual survival outside of hunting season on the logit scale due to changes in conspecific competition (Table 3.2). Dividing the size class-specific

range of the deviations of  $\phi_c$  from  $\phi_{0c}$  on the logit scale (numerator) by the range of the deviations of  $D_{ad+}$  from  $D_o$  on the log scale (denominator) provided the size class-specific slope parameter values:

$$b_c = \frac{\left( \left( \text{logit}(\phi_{c_{\max}}) - \text{logit}(\phi_{0c}) \right) \right) - \left( \text{logit}(\phi_{c_{\min}}) - \text{logit}(\phi_{0c}) \right)}{\log_{10} \left( \frac{D_{\min}}{D_o} \right) - \log_{10} \left( \frac{D_{\max}}{D_o} \right)}$$

**Senescence.** To prevent simulated alligators from living an unnaturally long life, e.g., > 100 years, I increased mortality rates for long-lived individuals as a form of senescence. Alligators cease growing around forty years old, with females reaching the milestone a few early earlier than males (Wilkinson et al., 2016). In the population simulation model, once an individual reached forty years old, regardless of their sex or TL, annual survival outside of the hunting season ( $\phi_{i,t}$ ) dropped to 0.6, then decreased linearly each year until it reached 0.01 or the individual died, whichever occurred first. Thus, annual survival outside of hunting season for individual  $i$  in year  $t$  is  $s_{i,t} \sim \text{Bernoulli}(\phi_{i,t})$  (Figure 3.2 and Figure 3.3). For individuals less than or equal to forty years old  $\phi_{i,t}$  and  $\phi_{c,t}$  are equivalent. Thereafter,  $\phi_{i,t}$  is a function of  $\text{age}_{i,t}$  into account;  $\phi_{i,t} \neq \phi_{c,t}$ .

$$\phi_{i,t} = \begin{cases} \phi_{c,t} & , \text{age}_i < 40 \\ \max \left( 0.01, 0.6 - 0.59 \cdot \frac{\text{age}_i - 40}{75 - 40} \right) & , \text{age}_i \geq 40 \end{cases}$$

The denominator is the range, in years, between the age when an alligator reaches maximum size and an upper limit for life expectancy (35 years). Although differences between males and females exist, with the range for females being closer to 30 years and for males being closer to 40 years, the same value, 35 years, was used for both sexes (Wilkinson et al., 2016).

## **Nesting and Recruitment.**

**Puberty.** Annual reproduction occurs in summer by the sexually mature adult female population, which survived annual harvest and non-harvest mortality processes. (i.e., females with  $TL_{i,t} \geq 183$  cm,  $h_{i,t} = 0$  and  $s_{i,t} = 1$ ),  $N_{FM,t}$ . In both nature and the population simulation model, not all adult-size females ( $\geq 183$  cm TL) are sexually mature. The minimum size and minimum age of females at sexual maturity, and the proportion of the female population at a given size that is sexually mature, are known to vary among alligator populations (Woodward et al., 1992).

Prior to nesting each summer in the population simulation model, immature adult females were subjected to a binomial puberty process. The probability that a female becomes sexually mature in a given year ( $\rho_M$ ) was then modeled on the logit scale as a function of female size (TL). Each year,  $\rho_{M_i}$ , the probability that female  $i$  reaches sexual maturity, increases due to changes in  $TL_{i,t}$  from annual growth between nesting seasons. If an adult female did not become sexually mature in  $t$ , she repeats the binomial puberty process again in  $t + 1$  and each year thereafter until she is successful or died. Once a female reached maturity, she had the potential to nest each summer until she was removed from the population through harvest or a non-harvest source of mortality.

For the predictive model relating  $\rho_M$  to size (TL),  $\rho_{M_i}$  for immature female  $i$  depended on the how far  $TL_{i,t}$  deviated from  $TL_0$ , the size at which female maturity probability is 0.5, on the logit scale. During the experimental harvest study at OL, the proportion of harvested adult females that were sexually mature was 0.75 and 0.98 at TLs 213 and 244 cm, respectively (Woodward et al., 1992). Treating the proportions of harvested adult females that were sexually mature as puberty probabilities, these values provided two points,  $(TL_{213cm}, \rho_{M213cm})$  and

( $TL_{244cm}$ ,  $\rho_{M244cm}$ ). With these points, I solved for the parameters in the equation  $\text{logit}(\rho_M) = b_{OL} (TL - TL_0)$  (Woodward et al., 1992). More specifically, I transformed the puberty probabilities to the logit scale, then computed the slope ( $b_{OL} = 0.08713$ ) and intercept ( $b_0 = -17.466$ ) for a basic logit-linear model between the two points. I then expressed the model using an x-offset ( $\text{logit}(\rho_M) = b_{OL}(TL - (-b_0/b_{OL}))$ ) rather than a y-intercept ( $\text{logit}(\rho_M) = b_0 + b_1x$ ). In this case, it was a TL-offset ( $TL_0 = 200.4529$  cm).

$$\text{logit}(\rho_{M_i}) = b_{OL}(TL_{i,t} - TL_0)$$

**Density Dependence.** I hypothesized that the increase in juvenile alligators observed over the course of the experimental harvest at OL resulted from adult female alligators becoming sexually mature, thus able to nest, at smaller sizes. Removal of adult females through harvest may have reduced competition for nesting sites and food, thereby releasing resources for smaller pubescent alligators. In the simulation model, puberty probability on the logit scale,  $\text{logit}(\rho_{M_i})$ , was related to changes in  $D_{ad^+,t}$  through a density-dependent linear shift in the puberty probability function (Figure 3.5). As  $D_{ad^+}$  decreases, the TL at which  $\rho_M$  equals 0.50 ( $TL_0$ , above) becomes smaller. Immature adult females of any size are then more likely to reach sexual maturity.  $TL_0$  is replaced by  $TL_D$ , the density-dependent TL-offset in the puberty probability function.  $TL_D$  is updated annually by adjusting  $TL_0$  by the product of the deviation of  $D_{ad^+,t}$  from  $D_0$  on the  $\log_{10}$  scale and the slope parameter  $b_D$ , such that  $TL_D = TL_0 + b_D (\log_{10}(D_{ad^+,t}) - \log_{10}(D_0))$ .

The slope,  $b_D$ , was derived by first assuming the TL at which  $\rho_M$  equals 0.5 may shift up to 10% in either direction from  $TL_0$ , from 180.41 to 220.50 cm TL, expressed as deviations from  $TL_0$ . Then, I set  $b_D$  equal to the difference between the range of TL-deviations from  $TL_0$  spanned by these values (40.09) and the range of adult<sup>+</sup> densities expressed as deviations from  $D_0$  on the

$\log_{10}$  scale that was used in the denominator in the equation for  $b_c$  (0.468):  $b_D = 39.622$ . Setting  $b_D$  equal to 0 turns off the density-dependent effect on  $\rho_M$ . Altogether the model for density-dependent puberty included:

$$\text{logit}(\rho_{M_i}) = b_{OL}(\text{TL}_{i,t} - \text{TL}_D)$$

$$\text{TL}_D = \text{TL}_0 + b_D (\log_{10}(\text{D}_{ad^+,t}) - \log_{10}(\text{D}_0))$$

$$\text{D}_{ad^+,t} = \text{N}_{ad^+,t,\text{postH}} / \text{A}_{OL}$$

**Nesting.** The number of nesting females each summer ( $\text{N}_{Fn,t}$ ) was modeled as a Bernoulli trial whereby each mature female in the population ( $n = \text{N}_{FM,t}$ ) had the same probability of nesting,  $\rho_{nest}$  (Figure 3.3). The value used for  $\rho_{nest}$  (0.398) came from the proportion of mature females ovulating, i.e., estimated probability of being postpartum, during the experimental harvest at Orange Lake (Woodward et al., 1992). A subsequent Bernoulli trial determined whether each nesting female's nest survived until eggs were ready to hatch using nest survival probability,  $\phi_{nest}$ . This determined the total number of surviving nests with clutches in  $t$  ( $\text{N}_{nests,t}$ ). The value for nest survival (0.452) came from the estimated mean nest survival rate at OL for the experimental harvest's mean year, 1985.5 (Woodward et al., 1992).

$$\text{N}_{Fn,t} \sim \text{Binomial}(\text{N}_{FM,t}, \rho_{nest})$$

$$\text{N}_{nests,t} \sim \text{Binomial}(\text{N}_{Fn,t}, \phi_{nest})$$

A Poisson process model determined the number of eggs produced in surviving nests ( $\text{N}_{eggs,t}$ ) based on  $\text{N}_{nests,t}$  and an expected clutch size ( $\mu_{clutch}$ ). I set  $\mu_{clutch}$  to 33 based on the average (of annual median values for 1982 - 1990) estimated mean clutch size for Orange Lake for the midpoint year 1985.5, 32.8 (Woodward et al., 1992). A binomial process model then determined the total number of eggs to survive and hatch ( $\text{N}_{recruits,t}$ ) based on an egg survival probability  $\phi_{egg}$ . For  $\phi_{egg}$ , I used 0.875, the median viability rate for all experimental harvest

study areas combined based on the survival rate of incubated eggs ( $n = 59$ ) to day 40 (Woodward et al., 1992). Before entering the population as hatchlings in fall  $t + 1$ , each of the  $N_{recruits,t}$  is assigned a sex and initial TL using the same process and parameter values used for hatchlings in the founder population (Table 3.1).

$$N_{eggs,t} \sim \text{Poisson}(N_{nests,t} * \mu_{Clutch})$$

$$N_{recruits,t} \sim \text{Binomial}(N_{eggs,t}, \phi_{egg})$$

**Growth.** In north-central Florida, alligators reach their maximum annual length and weight between September and November. Growth ceases between November and March, then recommences in April (Woodward et al., 1992). In my simulation, conditional on survival ( $s_{i,t} = 1$ ), individuals' TL increases through a growth process based on an alligator growth model estimated for alligators in South Carolina (Wilkinson et al., 2016). The Baker-form of the Schnute (1981) growth equation is typically fitted to mark-recapture data (Baker et al., 1991; Schnute, 1981). The original Wilkinson et al. (2016) growth model was parameterized in terms of snout-vent length (SVL, cm) rather than TL, so TL values were converted to SVL for the growth process, then back to TL after growth, using a conversion function estimated from alligators harvested on treatment lakes during the experimental harvest:  $TL = \alpha_s (SVL)^{\beta_s}$ . The  $s$  subscript indicates the intercept ( $\alpha_s$ ) and power coefficient ( $\beta_s$ ) in the conversion function were sex-specific (Woodward et al., 1992).

$$TL = \alpha_s SVL^{\beta_s}$$

$$SVL = \sqrt[\beta_s]{\frac{TL}{\alpha_s}} = \left(\frac{TL}{\alpha_s}\right)^{\frac{1}{\beta_s}}$$

I used the growth model equation with sex-specific parameter values from Wilkinson et al. (2016) to compute an expected size after growth for each individual ( $SVL_{i,(t+1)}$ ), based on size

before growth,  $SVL_{i,t}$  (Table 3.3). Individuals' size after growth,  $SVL_{i,(t+1)}$ , was a random variable drawn from a truncated Normal distribution centered on  $SVL_{i,(t+1)}$  with variance  $\epsilon_{sex}$ . The variance term represents parametric uncertainty derived from a Bayesian estimation of parametric uncertainty in growth projections (Lawson et al., 2022). The distribution was truncated at the lower end by current size (i.e.,  $SVL_{i,t}$ ) to prevent projections of size shrinkage. When an individual's new size exceeded terminal length ( $y_{2,sex}$ ), growth ceased, and the individual maintained its current size until it was removed from the population through harvest or non-harvest mortality. Individuals begin fall  $t+1$  in size class  $c$  based on their post-growth size:  $TL_{i,(t+1)} = (s_{i,t} \cdot \delta_{i,t})(1 - h_{i,t})$ .

$$SVL_i^0 = \left\{ \left( (SVL_{i,t}^{b_{sex}} e^{-(a_{sex}\Delta)}) + \left( y_{2,sex}^{b_{sex}} - y_1^{b_{sex}} e^{-(a_{sex}(\tau_2-\tau_1))} \left( \frac{1 - e^{-(a_{sex}\Delta)}}{1 - e^{-(a_{sex}(\tau_2-\tau_1))}} \right) \right) \right) \right\}^{1/b_{sex}}$$

$$SVL_{i,(t+1)}^0 = \max(SVL_{i,t}, \text{Normal}(SVL_i^0, \sqrt{\epsilon_{sex}}))$$

$$SVL_{i,(t+1)} = \begin{cases} SVL_{i,(t+1)}^0, & SVL_{i,t} \leq y_{2,sex} \\ SVL_{i,t}, & SVL_{i,t} > y_{2,sex} \end{cases}$$

$$\delta_{i,t} = \alpha_{sex_i} \cdot SVL_{i,(t+1)}^{\beta_{sex_i}}$$

**Harvest.** Harvest is initiated in fall  $t_{H0}$ . After annual growth and size class transitions, and recruitment of new hatchlings into the population, subadult<sup>+</sup> alligators were subject to harvest mortality. I simulated harvest in three steps. First, to implement a 13% proportional harvest of subadult<sup>+</sup> alligators, I used a binomial process model with a harvest probability equal to 0.13 ( $\lambda = 0.13$ ) to produce a value for how many harvestable alligators ( $N_{sa+,t}$ ) were expected to be harvested in year  $t$ ,  $\hat{H}_t$ . Second, I simulated partial controllability in harvest implementation using a binomial process that assumed the probability of hunter success was equal to 0.875. During the experimental harvest, the average hunter success rate (i.e., percentage of the annual

harvest quota taken by hunters, averaged over all years of the study, 1981 – 1990) was 87.5% (Woodward et al., 1992). Last, the harvest process was implemented to produce realized total take for year  $t$  ( $H_t$ ) by selecting  $n = H_t$  population members with  $TL \geq 122$  cm at random and removing them from the population.

$$H_t \sim \text{Binomial}(N_{sa^+,t,fall}, 0.875 \cdot \lambda)$$

### ***Data Simulation***

Using the alligator population simulation model, I generated multiple stochastic realizations of the latent alligator population characterized by the system processes and parameter values specified in the Population Model section, above. Each replicate realization differs slightly from the next due to demographic stochasticity and density dependence in state transition processes, e.g., survival and reproduction. To capture a range of possible stochastic realizations of the population, I simulated 100 population time series. From each time series, I saved life history records for individual alligators and annual summaries of population change to simulate a corresponding IPM data set. Ultimately, due to long model run times when fitting the estimation model to a set of IPM data, the results and conclusions presented in this chapter are based on ten ( $n = 10$ ) of the one-hundred replicate data sets originally simulated. Each IPM data set contained of four types of demographic data simulated from the first ten years of harvest, including: (1) eleven years of mark-recapture-recovery (MRR) data, (2) eleven years of count survey data, (3) ten years of nesting data, and (4) ten years of harvest data. These data represented the alligator population at Orange Lake, FL between 1981-1990, during the FFWCC's experimental harvest.

An advantage of using simulation is that it allows me to conduct my analysis multiple times, making inference about performance of the IPM more robust to spurious outcomes arising

by chance. Each trial consists of fitting the estimation model to a set of IPM data. Repeated trials make it possible to identify expected outcomes as well as a range of possible outcomes that can emerge purely by chance. Variability among replicate IPM data sets arises from stochasticity in both population state and observation processes. As noted earlier, a benefit of SSMs is their ability to distinguish among variability arising from system and observation processes to improve parameter estimates. Next, I describe the observation process used to create each of the four types of demographic data in an IPM data set.

**Mark-Recapture-Recovery.** Members of the simulated alligator population alive in summer during the first ten years of the simulated study period were selected at random for inclusion in the simulated MRR dataset. The number of individuals captured, marked, and released in the simulated population in each size class, each year, was based on the number of alligators in each size class initially captured, marked, and released by the FFWCC between April and July 1980 – 1989 (Table 3.4). Recaptures and recoveries were simulated for years two through eleven of the study period (i.e.,  $(t_{H0}+1):(t_{H0}+10)$ ). For each “marked” individual in the simulated dataset, I generated a capture history by using an annual binomial process with size-specific recapture probabilities ( $p_c$ ) to decide whether the individual was observed after their initial release (Table 3.5). Individuals that were harvested during the study period were recovered without error.

Once recaptured or recovered, individual latent state ( $z_{i,t}$ ) was recorded, and recaptured individuals were re-released. Nine latent states were specified. One through five corresponded to individuals alive in size class  $c$  ( $z = 1:5$ , respectively). Latent states six, seven, and eight correspond to individuals that were recently harvested (during hunting season  $t - 1$ ) from the subadult, adult, or bull size class, respectively. Latent state nine represented an absorbing state

for dead individuals, including individuals that died prior to the start of  $t - 1$ , individuals that died from non-harvest mortality during  $t - 1$ , and individuals harvested in  $t - 2$  that were observed in one or the recently harvested states ( $z = 6:8$ ) at the beginning of  $t - 1$ . In the creation of MRR data, occasions when individuals were not observed were coded with nine. To clarify, latent state  $z_{i,t} = 9$  means individual  $i$  is dead in summer  $t$ , while an observed state  $z_{obs,i,t} = 9$  means the state of the individual is unknown. Individuals may not be observed because they are dead, or they are alive but were not recaptured or recovered in  $t$ . In the IPM, I used a marginalized latent state formulation in the MRR likelihood (Yackulic et al., 2020).

**Count Survey Data.** Annual monitoring data from summer count surveys were simulated over an eleven-year period with two replicate surveys per year ( $Y_{c,t,j}$ , for  $c = (1, 2, \dots, 5)$ ,  $t = (1, 2, \dots, T)$ , and  $j = (1 \text{ and } 2)$ ). The first year of count data corresponds to the population in the summer preceding the first hunting season in  $t_{H0}$ . Size class-specific counts for annual survey replicates were drawn from a binomial distribution that sampled from latent summer size class abundances ( $N_{c,t,summ}$ ) using size class and survey replicate-specific detection probabilities ( $p_{C_{c,t,j}}$ ):  $Y_{c,t,j} \sim \text{Binomial}(N_{c,t,summ}, p_{C_{c,t,j}})$

Detection probabilities ( $p_{C_{c,t,j}}$ ) were calculated for each annual replicate survey using a logit-linear model that related water level covariate data for each replicate survey to detection probability for each size class:  $\text{logit}(p_{C_{c,t,j}}) = \beta_{1,c} + \beta_{2,c} \text{cWL}_{t,j} + \beta_{3,c} \text{cWL}_{t,j}^2$  (Figure 3.6, Table 3.6). Covariate data were generated to account for the effects of the survey environment on detection probability. More specifically, I simulated eleven years of water level data (WL, ft), two observations per year, one for each replicate count survey. For small and large size classes, detection probability decreases as water levels rise (Fujisaki et al., 2011). High water conditions facilitate dispersal into other suitable habitats than those established as regular survey routes.

Small alligators are more likely to find cover for safety (Fujisaki et al., 2011; Woodward et al., 1987) while larger alligators are more likely to submerge (Bugbee, 2008; Fujisaki et al., 2011). Mass-dependent rates of oxygen consumption enable longer dives by big animals (Fujisaki et al., 2011; Wright, 1987). For each size class, combinations of values were plugged into the quadratic model linking detection probability on the logit scale to a range of WL values informed by water level data and its temporal variability at Orange Lake during the study period (Normandeau Associates, 2016; Woodward et al., 1992). The final selection of  $\beta_{1:3,c}$  values were deemed sufficient for producing alligator detection probabilities that decreased with increasing water level and the effect of WL on detection probability (i.e., rate of change) was greater for small compared to large size classes over the range of WL values observed at OL between 1980 and 1991 (Fujisaki et al. 2011) (Figure 3.6, Table 3.6, Appendix B).

**Nesting Data.** Annual summer reproductive data consisted of the number of nests counted ( $R_t$ ) and the total number of eggs in counted nests, ( $J_t$ ). Nest counts,  $R_t$ , were drawn from a binomial distribution with the probability of detecting a nest with a clutch ( $p_{CL}$ ) equal to 0.94 based on the estimated mean percentage of nests sighted during initial aerial nest searches on OL during the experimental harvest (94%) (Woodward et al., 1992). Then, a random sample of nests ( $n = R_t$ ) was selected from the clutch records for the latent population in summer  $t$ . Then I summed the clutch sizes in that sample of latent population nests and used that for  $J_t$ .  $J_t$  is the total number of eggs laid in counted clutches, prior to the egg survival process that produces hatchling recruits for the population in fall  $t + 1$ .

$$R_t \sim \text{Binomial}(N_{nests,t}, p_{CL})$$

$$J_t \sim \sum_{i=1}^{R_t} N_{eggs,R_{t,i}}$$

**Harvest Data.** Harvest count data were also simulated under the assumption the harvest mortality process is partially observable. Accordingly, annual counts of alligators removed from the population by harvest depended on the probability a hunter reports his harvest,  $r_H$  harvest report rate. Working under the assumption most hunters report their harvest and that rate of reporting is not dependent on animal size, I set  $r_H$  to 0.90 (90%). Annual harvest counts ( $y_{H_{hc,t}}$ ) were generated from a binomial distribution with sample size equal to the number of alligators harvested from the latent population each year by size-structured harvest class ( $H_{hc,t}$ ) and probability equal to a hunter harvest reporting rate,  $r_H$ :  $y_{H_{hc,t}} \sim \text{Binomial}(H_{hc,t}, r_H)$ . The harvest class index ( $hc$ ) takes on values 1, 2, or 3 corresponding to subadult, adult, and bull size classes ( $c = 3$  (subadult), 4 (adult), or 5 (bull)), respectively. In terms of latent states, harvest classes ( $hc$ ) correspond to  $z = 6, 7, \text{ or } 8$ , respectively.

### ***Estimation Model***

The alligator IPM followed the same sequence of annual system processes as described in the population simulation model used to generate latent population records, except annual time steps begin in summer in the estimation model rather than the fall. The estimation model begins each year ( $t$ ) in summer, during the nesting period, but before growth processes, to align with the data from eyeshine surveys and nest counts, and mark-recapture data. The population generating (simulation) model, which was created before the data simulation or estimation models, initiates the annual cycle in fall, after summer size-class transitions and recruitment. As in the simulation model, the population is structured by latent state,  $z$ . The first five states are alligators alive in one of the five size classes ( $c$ ). The next three states,  $z = 6, 7, \text{ and } 8$ , correspond to alligators recently harvested as subadult, adult, or bull, respectively. Latent state  $z = 9$  is an absorbing state

for all dead individuals removed from the population through non-harvest mortality and recently harvested individuals.

The estimation model tracks alligators through state transitions over the first ten years of harvest, beginning the summer preceding the first fall hunting season. All system processes (size class transitions, harvest, survival, and reproduction) are stochastic, modeled as binomial or Poisson processes. A summer population census initiates the annual cycle ( $N_{z,t,summ}$ ). At the start of the model, summer  $t = 1$ , the population is distributed among latent states  $z \leq 5$  (alive in size class  $c \leq 5$ ). For  $z = 6, 7, 8$ , and  $9$ ,  $N_{z,1,summ}$  is 0 (none of the population is recently harvested or dead).

Between summer and fall, growth and reproductive processes occur. Then, some members of the population alive in latent states  $z = 1, 2, \dots$ , or  $5$  (corresponding to size classes,  $c = 1, 2, \dots$ , or  $5$ ) transition to the next larger size class by fall ( $N_{tr,c}$ ). The process was represented in the model using a binomial size-class specific transition probability ( $\psi_c$ ) such that  $N_{tr,c} \sim \text{Binomial}(N_{c,t,summ}, \psi_c)$ , for  $c \leq 4$ . Before size class transitions, a portion of the adult<sup>+</sup> population composed of sexually mature females build nests ( $N_{nests,t} \sim \text{Binomial}(N_{ad+,t,summ}, p_{FMN})$ ). Each nesting female lays a clutch of eggs; clutch size, CL. Depending on egg survival ( $\phi_{egg}$ ), which accounts for both nest survival and egg viability, eggs successfully hatch new recruits ( $N_{recruits,t} \sim \text{Binomial}(N_{eggs,t}, \phi_{egg})$ ). Recruits join the population in fall as hatchlings ( $N_{I,t,fall} = N_{I,t,summ} - N_{tr,1,t} + N_{recruits,t}$ ).

By fall  $t$ , members of the population that were alive at the beginning of summer remain in the same size class ( $c$ ) or they transitioned to the next ( $c + 1$ ), and hatchlings produced by summer nests enter the population. Any individuals in recently harvested states ( $z = 6, 7$ , or  $8$ ) in

summer transition to the dead absorbing state  $z = 9$  by fall where they stay for the remainder of the time series.

$$N_{1,t,fall} = N_{1,t,summ} - N_{tr,1,t} + N_{treruits,t}$$

$$N_{c,t,fall} = N_{c,t,summ} - N_{tr,c,t} + N_{tr,(c-1),t}, \text{ for } c = 2, 3, \text{ or } 4$$

$$N_{5,t,fall} = N_{5,t,summ} + N_{tr,4,t}$$

$$N_{6:8,t,fall} = 0$$

$$N_{9,t,fall} = N_{9,t,summ} + N_{6:8,t,summ}$$

Between fall  $t$  and the following summer  $t + 1$ , the population is subject to harvest and non-harvest sources of mortality. First, members of subadult<sup>+</sup> size classes ( $c = 3, 4, \text{ or } 5$ ) are subject to harvest mortality with a constant harvest probability,  $\lambda$ :  $H_{hc,t} \sim \text{Binomial}(N_{c,t,fall}, \lambda)$ . After harvest,  $n = H_{hc,t}$  alligators are removed from the corresponding size classes:  $N_{c,t,postH} = N_{c,t,fall} - H_{hc,t}$ , and assigned to the appropriate recently-harvested state,  $z = 6, 7, \text{ or } 8$ :  $N_{z,t,postH} = H_{hc,t}$ . Remaining population members are then subject to non-harvest sources of mortality in the annual survival process outside of the hunting season with temporally variable size class-specific survival probability  $\phi_{c,t}$ :  $N_{c,(t+1),summ} \sim \text{Binomial}(N_{c,t,postH}, \phi_{c,t})$ .

At the beginning of the next annual cycle, summer  $t + 1$ , individuals harvested during hunting season (fall  $t$ ) remain in one of the recently harvested states ( $N_{z,t,summ} = N_{z,t,postH}$ , for  $z = 6, 7, \text{ or } 8$ ). Population members alive in size class  $c \leq 5$  ( $N_{z,(t+1),summ}$ , where  $z = c$ ) survived both hunting season and the annual survival process outside of hunting season. Individuals alive after hunting season that succumbed to mortality during the post-harvest survival process are moved to the dead absorbing state  $z = 9$  ( $N_{9,(t+1),summ} = N_{9,t,postH} + (N_{z,t,postH} - N_{z,(t+1),summ})$ , for  $z = c \leq 5$ ).

## Data Likelihoods.

**Marginalized MRR Likelihood.** For the MRR data likelihood, I followed the marginalized latent state approach described by Yackulic et al. (2020) because it is more computationally efficient than the traditional discrete latent state formulation for the Cormack-Jolly-Seber model (Yackulic et al., 2020). Depending on how discrete latent states are simulated, Bayesian population models can be very slow. Marginalized code is faster and has less bias than an N-augmentation approach and estimates for parameters and derived quantities such as abundance are minimally affected (Yackulic et al., 2020).

In the marginalized approach, capture records are specified in terms of a matrix,  $\text{rrCH}$ , containing the set of unique capture segments observed among individual MRR capture histories during the study period. Individual capture histories were broken down into capture history segments consisting of paired observations, one observation is the latent state at the release occasion ( $t = \text{first}_k$ ) and the other is the latent state at the subsequent recapture or recovery occasion ( $t = \text{last}_k$ ). Then, a copy of each unique capture segment ( $k$ ) observed among individuals sampled in the MRR data set was compiled into a capture array ( $\text{rrCH}$ ). For capture occasions in between the  $\text{first}_k$  and  $\text{last}_k$  observations,  $\text{rrCH}_{k,t}$  was coded with 9 for unobserved (i.e., not recaptured or recovered). For segments that only contained a  $\text{first}_k$  observation, the  $\text{last}_k$  observation was set equal to the last year of the study ( $T$ ) and  $\text{rrCH}_{k,T}$  was coded as unobserved, i.e.,  $\text{rrCH}_{k,t} = 9$ . In addition to the data matrix  $\text{rrCH}$ , the estimation model considers  $\text{rrFR}_k$ ; the number of times each  $k$  segment appeared in the MRR data set, or the frequency of occurrence of unique capture segment  $k$  among all individuals' capture histories.

In the analysis, the estimation model loops through each segment (vector  $\text{rrCH}_k$ ), populating a transition probability matrix,  $p_z$ , that integrates state transition ( $\mathbf{tr}$ ) and recapture

(**rho**) probabilities over time based on  $z_{obs,first_k}$  and  $z_{obs,last_k}$ , and the number of occasions elapsed between  $t = first_k$  and  $t = last_k$ . The dimensions of  $pz$  correspond to capture segment ( $k = 1, 2, \dots, N_{rrCH}$ ), year ( $t = 1, 2, \dots, T$ ), and state ( $z = 1, 2, \dots, 9$ ).

Beginning with  $t = first_k$ , the model assigns a probability of 1 to the element of vector  $pz_{k,first_k}$  that corresponds with observed state  $z = rrCH_{k,first_k}$ , thus  $pz_{k,first_k,rrCH_{k,first_k}} = 1$ . A probability of 0 is assigned to all other states on that occasion. Then, looping forward through time, over each capture occasion preceding  $last_k$  ( $t = (first_k + 1):(last_k - 1)$ ),  $pz_k$  is populated by multiplying matrix  $pz$  for  $t-1$  by the state transition matrix **tr**, which contains annual survival ( $\phi$ ), transition ( $\psi$ ), and harvest ( $\lambda$ ) probabilities (Figure 3.7). The inner product of those two is then multiplied by the observation matrix **rho**, which contains recapture probabilities ( $p_c$ ) (Figure 3.7). Elements of **rho** correspond to probabilities of the observed state  $z_{obs,(t+1)}$  given latent state  $z_t$ .

The probability of the observed state at the last record of  $rrCH_k$  given latent state  $z$  at the occasion of recapture or recovery,  $P(z/z_{obs,last_k})$  or  $P(9|z_{obs,last_k})$  if no observations followed  $first_k$ , is the cumulative sum of the probabilities of being observed in each state on occasion  $last_k$  ( $lik_k$ ). Using a variation on the "ones trick" for JAGS, the cumulative likelihood for segment  $rrCH_k$  ( $lik_k$ ) is then sampled from a binomial distribution based on its frequency among individual capture histories in the MRR dataset ( $rrFR_k$ ), which yields a scaled probability of the likelihood ( $one_k$ ).

$$pz_{k,(t+1),z} = (pz_{k,t,1:9} \cdot \mathbf{tr}_{1:9,t,z}) \times \mathbf{rho}_{z_t,t,z_{obs,(t+1)}}$$

$$lik_k = \sum_{z=1}^9 pz_{k,last_k,z}$$

$$one_k \sim \text{Binomial}(rrFR_k, lik_k)$$

**Count Data Likelihood.** The likelihood for count survey data mirrored the data simulation process described above. For each summer  $t$  ( $n = 11$ ), survey replicate  $j$  ( $n = 2$ ), and size class  $c$  ( $n = 5$ ), count data,  $Y_{c,t,j}$ , were modeled as coming from a binomial distribution with a sample size equal to the latent size class abundance at the beginning of summer ( $N_{c,t,summ}$ , for  $c = z = 1, 2, \dots, 5$ ) and detection probability  $p_{C_{t,j,c}}$ . Values for  $p_{C_{t,j,c}}$  on the logit scale were related to covariate centered water level data ( $cWL_{t,j}$ ) through a quadratic function with size-specific coefficients:

$$\text{logit}(p_{C_{t,j,c}}) = \beta_{1,c} + \beta_{2,c}cWL_{t,j} + \beta_{3,c}cWL_{t,j}^2$$

$$Y_{c,t,j} \sim \text{Binomial}(N_{c,t,summ}, p_{C_{t,j,c}})$$

**Nesting Data Likelihood.** The number of nests observed each summer ( $R_t$  for  $t = 1, 2, \dots, T$ ) was modeled as a binomial random variable with a sample size equal to the latent number of nests in the population,  $N_{nests,t}$ , and a nest, or clutch, detection probability,  $p_{CL}$ :  $R_t \sim \text{Binomial}(N_{nests,t}, p_{CL})$ . The total number of eggs counted each summer,  $J_t$ , from observed nests is a subset of the total number of eggs produced by all clutches in summer  $t$ ,  $N_{egg,t}$ . I described  $J_t$  using a Poisson distribution with the mean equal to the product of the number of observed clutches ( $R_t$ ) and the expected clutch size ( $CL_t$ ) for OL alligators:  $J_t \sim \text{Poisson}(R_t * CL_t)$ . I modeled expected clutch size as a temporally random variable drawn from a normal distribution with the grand mean clutch size  $\mu_{CL}$  and SD  $\sigma_{\mu_{CL}}$ . In the state-space process model,  $N_{egg,t}$  was then defined as the sum of the total number of eggs observed in nests,  $J_t$ , and the product of  $CL_t$  and the number of nests unobserved in summer  $t$ :  $N_{egg,t} = J_t + (N_{nests,t} - R_t) \cdot CL_t$ .

**Harvest Data Likelihood.** The likelihood for harvest data mirrored its simulation process. The number of hunter harvested alligators counted in harvest class  $hc$  each fall  $t$  ( $n = 10$ ),  $yH_{hc,t}$ , were described as coming from a binomial distribution with a sample size equal to the latent

number of alligators removed from the population during hunting season  $t$  ( $H_{hc,t}$ , for  $hc = 1, 2, 3$ , equal to  $c = 3, 4, 5$ ) and a reporting rate ( $r_H$ ).

**Prior Distributions.** Prior distributions were assigned to all unknown quantities in the model, including latent effects and parameters such as demographic rates and observation errors. Annual size class-specific survival probabilities ( $\phi_{c,t}$ ), were defined as random (temporal) effects drawn from a normal distribution with mean equal to  $\bar{\phi}_c$  and precision  $\tau_{\phi_c}$ , truncated to the probability scale (0, 1). The normal distribution in JAGS uses precision  $\tau$ , which is equal to one divided by the variance ( $= 1/\sigma^2$ ), to describe variability around the mean. I converted  $\tau_{\phi_c}$  values to SD ( $\sigma_{\bar{\phi}_c}$ ), and I assigned uninformative uniform prior distributions to the hyperparameters  $\bar{\phi}_c$  and  $\sigma_{\bar{\phi}_c}$ , as well as egg survival probability  $\phi_{egg}$  (Table 3.7). A normal prior distribution was assigned to expected clutch size,  $CL_t \sim \text{Normal}(\mu_{CL}, \tau_{\mu_{CL}})$ . Slightly informative uniform priors were then assigned to the hyperparameters  $\mu_{CL}$  and  $\sigma_{\mu_{CL}} (= 1/\tau_{\mu_{CL}})$  based on existing research (Table 3.7). Vague, or uninformative, uniform prior distributions were assigned to the proportion of the adult<sup>+</sup> population that is mature nesting females each summer,  $p_{FMN}$ , nest detection probability,  $p_{CL}$ , size class-specific transition probabilities,  $\psi_c$ , and recapture rates,  $p_c$  (Table 3.7). Uninformative normal distributions were used for count survey detection probability model parameters,  $\beta_{1:3,c}$  (Table 3.7). Slightly informative, weak, uniform distributions were used for harvest probability,  $\lambda$ , and hunter harvest reporting rate,  $r_H$ .

Prior distributions were assigned to initial population state abundances as well because Markovian population state processes cannot be applied to the population at the beginning of the time series (summer,  $t = 1$ ),  $N_{z,1,summ}$ . I used the Dirichlet distribution to sample the number of individuals in size class  $c$ ,  $N_{c,1,summ}$ , as follows. I drew values  $X_c$  from a gamma distribution with shape parameter  $k$  and scale parameter  $\theta$ . I set  $\theta$  equal to 1 and  $k$  equal to the proportion of the

total population in each size class,  $pN_{0c}$ . I computed values for  $pN_{0c}$  using the initial population size class abundances from the population simulation model ( $N_{0c}$ , Table 3.1), which were read into the model as data. I then sampled values of  $pN_{0c}$  by dividing  $X_c$  by the sum of  $X_c$  for all  $c$  (1, 2, ..., 5). Then, initial size class abundances,  $N_{z,1,summ}$  for  $z = c \leq 5$ , were set equal to the product of  $pN_{0c}$  and the latent total initial population size,  $N_0$ . A weakly uniform prior was assigned to  $N_0$  (Table 3.7), and abundances for recently harvested and dead latent states ( $z = 6, 7, 8, 9$ , respectively) were set to 0. R code for the population simulation model (Appendix C) and data simulation (observation) models (Appendix D) are provided in the Appendices. A directed acyclic graph (DAG) for the estimation model is shown in Figure 3.8.

### ***Model Verification***

The IPM (estimation model) was specified and fitted to the data in JAGS (Just Another Gibbs Sampler) (Plummer, 2003) using the jagsUI package version 1.5.2 (Kellner & Meredith, 2021), a wrapper for Rjags 4.12 (Plummer et al., 2021), in the program R version 4.1.2 (R Core Team, 2021). In each trial ( $n = 10$ ), the model was fitted to a replicate IPM data set containing eleven years of MRR data, count survey data, and nesting data, and ten years of harvest data using the Rjags autojags function. I ran three Markov chain Monte Carlo (MCMC) chains with a 10,000 iteration-long adaptive phase for the MCMC sampler and a burn-in period of 50,000 iterations was discarded before monitoring posterior distributions. Initial values were supplied for each chain. See Appendix E for the JAGS estimation model code, R code for the initial values generating function, and initial values used for the three MCMC chains in each trial.

The estimation model ran in JAGS until values of the Brooks-Gelman-Rubin statistics ( $\hat{R}$ ) values were less than or equal to 1.1 or a maximum of 500,000 iterations completed.  $\hat{R}$  is the ratio of the spread of all posterior draws combined to the mean spread of each chain, and values

close to 1.0 suggest the chains are sampling from the posterior distribution properly.  $\hat{R}$  values were updated every 100,000 iterations and chains were not thinned. I also assessed quality of each posterior distribution by computing its effective sample size (N.eff), which estimates the information content in correlated draws from the posterior distribution. Posterior summary statistics presented in the Results section derive from the last 100,000 iterations of each trial.

For efficiency, not all unknown variables in the model were monitored. The expectation was to expand the list of monitored variables as time permitted, which it did not. The parameters that were monitored in the initial set of trials, and reported on below, included:  $\lambda$  (harvest probability),  $r_H$  (hunter harvest reporting rate),  $p_{FMN}$  (proportion of the latent adult+ population composed of nesting females),  $\mu_{CL}$  (expected clutch size),  $\sigma_{CL}$  (SD of expected clutch size),  $\phi_{egg}$  (egg survival probability),  $p_{CL}$  (nest/clutch detection probability),  $\psi_c$  (size class-specific transition probabilities),  $p_c$  (size class-specific recapture probabilities),  $\beta_{1:3,c}$  (size class-specific regression coefficients for the quadratic count survey detection probability model on the logit scale),  $\bar{\phi}_c$  (expected annual size class-specific survival probabilities), and  $\sigma\bar{\phi}_c$  (SD for the normal distribution centered on  $\bar{\phi}_c$  from which annual survival probabilities are drawn).

After each trial, convergence among MCMC chains ( $n = 3$ ) was checked quantitatively using the  $\hat{R}$  statistic, as well as visually by inspecting trace plots (Brooks & Gelman, 1998). I then considered model performance based on how well the model recovered (estimated) unknown parameters. Specifically, the 95% Bayesian credible interval (BCI), which spans the 2.5th and 97.5th percentiles of MCMC draws from the posterior distribution for each parameter, was checked to determine whether the true (latent) parameter value was contained therein (Table 3.8). The 95% BCI is the Bayesian analogue to the frequentist confidence interval; it contains the parameter of interest with a probability of 0.95 (Kéry & Schaub, 2012). Trial results were

compiled and the proportion of trials in which the latent parameter value fell within the 95% BCI are presented below by parameter.

For time invariant system process and observation process parameters specified *a priori*, a scalar value was compared to the posterior BCI across trials (Table 3.8). In contrast, for dynamic demographic parameters, i.e., those that varied over time within trials due to Markovian system processes and density-dependence, the BCIs for posterior parameter estimates were compared to trial-specific summaries of latent parameter values (Table 3.8).

Annual size-specific survival probabilities ( $\phi_{c,t}$ ), varied year-to-year due to density-dependence. To evaluate estimates for  $\bar{\phi}_c$ , within each trial, I computed the mean and SD of the expected annual size-specific survival probabilities generated each year of the simulated study period ( $\phi_{c,t}$ , for  $t = t_{H0} : t_{H0}+10$ ), which are produced each fall by a density-dependent function, prior to the annual survival process outside of hunting season. I used the trial-specific summary statistics as the basis for calculating the proportion of trials in which the 95% BCI of the posterior contained trial-specific latent values for  $\bar{\phi}_c$  and  $\sigma_{\bar{\phi}_c}$ .

Latent values for size class-specific transition rates ( $\psi_c$ ) and proportion of the adult<sup>+</sup> population made up of nesting adult females ( $p_{FMN}$ ), were calculated from trial-specific realized population records. In the population simulation model, individuals advance size classes as a function of the TL growth process that precedes each fall hunting season. For each trial, I first calculated the annual transition rate for each size class by dividing the number of individuals that survived through summer  $t$  and advanced to a larger size class for fall  $t$  by the total number of individuals in the size class in summer  $t$ . Then, I averaged the annual realized size class-specific transition rates over years  $t = t_{H0} : t_{H0}+10$  to produce a trial-specific mean annual transition rate for each size class. Posterior distribution 95% BCIs for size class-specific transition probabilities

were then examined, trial-by-trial, to see if they contained the mean rate computed from latent trial records. For  $p_{FMN}$ , within each trial, for each year in the study period, I divided the number of nesting females by the latent abundance of the adult<sup>+</sup> population in summer  $t$ , then averaged values over years and examined whether trial-specific posterior 95% BCIs contained trial-specific realized mean latent annual proportion of the ad<sup>+</sup> population constituted by nesting females.

## Results

### *Latent Population Time Series*

With density-dependent puberty and survival processes operating in the population as detailed in the Methods section, the population simulation model produces a self-sustaining population with or without a 13% proportional harvest (Figures 3.9, 3.10, 3.11, and 3.12). In the absence of harvest mortality (Figures 3.9 and 3.10, and Figures 3.11 and 3.12 before  $t_{H0}$ ) and after initiating an annual hunting season for subadult<sup>+</sup> alligators (Figures 3.11 and 3.12), abundances stabilize following an initial adjustment period, avoiding a population surge or crash.

### *Estimation Model Trials*

Here I present the results for ten trials ( $n = 10$ ) with IPM data sets simulated from the replicate population time series plotted in Figure 3.13. A summary of trial  $\hat{R}$  values is presented in Table 3.9 along with the proportion of trials in which the latent parameter value fell within the 95% BCI.  $\hat{R}$  values fell below 1.2 for most parameters in all trials except for  $p_{CL}$  ( $\hat{R} = 1.277$ ) in trial 3, and  $p_{FMN}$  ( $\hat{R} = 1.295$ ) and  $\phi_{egg}$  ( $\hat{R} = 1.279$ ) in trial 4 (Table 3.9). Averaged across trials by parameter, effective sample size of the posterior distribution (N.eff) ranged from 52.8 ( $\bar{\phi}_H$ ) to 166,834 ( $p_B$ ) (Table 3.9). On average, N.eff for  $p_{FMN}$  was 153.  $\hat{R}$  for  $p_{FMN}$  was less than 1.1 in most trials and MCMC chains were mixing, but they were unstable (Table 3.9). In trial 4,

MCMC chains for  $p_{FMN}$  were neither well mixed nor stable. On average, the effective sample size (N.eff), which is the number of independent draws from the posterior which would give the same precision as the MCMC chain we have, for  $\phi_{egg}$  was also small (109), and while trial  $\hat{R}$  values were typically less than 1.1 and MCMC chains were mixing, they were unstable (Table 3.9). Across trials,  $\hat{R}$  for expected annual hatchling survival ( $\bar{\phi}_H$ ) was less than 1.1, but N.eff tended to be less than 100 and MCMC chains were poorly mixed and unstable (Table 3.9).

Of the state process parameters monitored, the 95% BCI encompassed the latent parameter value in all ten trials for  $\bar{\phi}_{SA}$ ,  $\bar{\phi}_A$ ,  $\sigma_{\bar{\phi}_A}$ ,  $\psi_A$ ,  $\bar{\phi}_B$ ,  $\sigma_{\bar{\phi}_B}$ ,  $\sigma_{\bar{\phi}_H}$ ,  $\sigma_{\bar{\phi}_J}$  and  $\mu_{CL}$  (Table 3.9; Figures 3.14, 3.15, 3.16, and 3.17). In more than half of the trials, the 95% BCI encompassed the latent value  $\phi_{egg}$  (9 of 10),  $\bar{\phi}_J$  (8 of 10),  $\psi_H$  (8 of 10), and  $\psi_{SA}$  (7 of 10) (Table 3.9; Figures 3.14 and 3.15). Less than half of the trials produced 95% BCIs containing the latent value for  $\bar{\phi}_H$  (4 of 10),  $p_{FMN}$  (3 of 10),  $\sigma_{\bar{\phi}_{SA}}$  (2 of 10), and  $\lambda$  (1 of 10) (Figures 3.14, 3.18, and 3.19). Latent values for  $\psi_J$  and  $\sigma_{CL}$  fell outside of the 95% BCI in all ten trials (Table 3.9; Figures 3.15, 3.16, and 3.17).

Of observation processes parameters monitored, 95% BCIs contained latent parameter value in all ten trials for  $p_c$  ( $c \leq 5$ ) and  $\beta_{1:2,J}$  (Table 3.9; Figures 3.20 and 3.21). In at least half of the trials, the latent values for  $p_{CL}$  (9 of 10),  $\beta_{3,J}$  (9 of 10),  $\beta_{2,A/B}$  (8 of 10), and  $\beta_{3,A/B}$  (5 of 10), fell within the 95% BCI (Table 3.9; Figures 3.20 and 3.21). Less than five trials produced 95% BCI that included the latent value for  $\beta_{3,H}$  and  $\beta_{3,A/B}$  (3 of 10),  $\beta_{2,H}$  and  $\beta_{2,SA}$  (2 of 10),  $\beta_{3,SA}$  (2 of 10), and  $\beta_{1,H}$  (1 of 10) (Table 3.9; Figure 3.21). The 95% BCIs in none of the trials (0 of 10) contained the latent value for  $r_H$ ,  $\beta_{1,SA}$ , or  $\beta_{1,A/B}$  (Table 3.9; Figures 3.18 and 3.21).

## Discussion

This chapter set out to verify an integrated population model for alligators using simulation. A preliminary objective of the study was to develop a mechanistic alligator

population simulation model based on current scientific understanding of alligator population biology and capable of generating a self-sustaining population. This was accomplished by simulating individual life histories of population members based on an alligator growth model that increases individuals' TL over time conditional on their survival. Demographic processes (survival, reproduction, growth, harvest mortality) were stochastic, and size class-specific annual survival probabilities and puberty for adult females were density-dependent using stochastic demographic processes parameterized with values from existing alligator research from the population at Orange Lake, FL.

To my knowledge, this is the first alligator population simulation model that incorporates density-dependent feedback and does not forecast growth to infinity or population collapse upon the initiation of hunting. Simulating the latent population over 150 years, including 100 years with harvest in gives no indication of a future decline (Figures 3.11 and 3.12). Simulated time series are consistent with observations of real alligator populations that have persisted across the species' range in the years since agencies established recreational harvest programs, though the oldest is less than forty years old.

The IPM prototype (estimation model) I developed for this chapter contained no density-dependent mechanisms, whereas the latent population time series underlying trial data sets emerged from a population with density-dependent survival and puberty processes. Despite the lack of a density-dependent survival mechanism, the estimation model recovered annual survival probabilities for harvestable size classes ( $\bar{\phi}_{SA/AB}$ ) (Figure 3.14). It also did well recovering  $\bar{\phi}_J$  but had difficulty recovering  $\bar{\phi}_H$  in most of the trials. Whether or not the model-estimated posterior mean values are capable of (re)producing the latent population's dynamics under the system process model specified in the IPM remains to be seen. Arguably, this would be one of the most

critical evaluations of the model's usefulness. Such a determination requires simulating a population under the stated circumstances, then comparing the resulting time series to the latent population records produced by the population simulation model described in the Methods section.

The model did a poor job estimating the transition rate for juveniles, failing to recover the latent value in any of the trials (Figure 3.15). The reason is not immediately apparent but may be related to the model's inability to recover  $\sigma\bar{\phi}_{SA}$  (Table 3.9). In both cases,  $\psi_J$  and  $\sigma\bar{\phi}_{SA}$ , the model tended to overestimate the parameter value (Figures 3.15 and 3.16). The model did well estimating the SD of annual survival probabilities,  $\sigma\bar{\phi}_c$ , for all size classes except subadult (Figure 3.16).

In general, the model struggled to estimate parameters associated with population productivity (nesting and recruitment). The model consistently recovered mean clutch size ( $\mu_{CL}$ ) (Figure 3.17). Despite a weakly informative prior for  $\mu_{CL}$ , the posterior was driven by the likelihood and data. The model underestimated SD for expected clutch size,  $\sigma_{CL}$ . In the latent population model, clutch sizes are drawn from a Poisson distribution where the mean and variance parameters are equal, which results in SD for  $\mu_{CL}$  calculated from latent time series records as approximately six eggs (Figure 3.17). In the estimation model, clutch size is normally distributed, and a uniform prior was assigned to  $\sigma_{CL}$ .

Posterior distributions underestimated nest detection probability ( $p_{CL}$ ) and hatchling recapture probability ( $p_c$ ), but wide BCIs indicate a lot of uncertainty (Figure 3.20). When nest detection probability is underestimated, annual reproductive output (nests and eggs) may be overestimated. Underestimating hatchling recapture probability means we think survival is

higher than it really is, which is evidenced in Figure 3.14. Recapture probabilities for other size classes were often recovered, which may have contributed to the survival probabilities results.

The estimation model generally struggled to estimate the coefficient values for the WL-count survey detection probability model except for the juvenile size class for which all three detection model parameters ( $\beta_{1:3,j}$ ) were recovered (Figure 3.21). Estimates of annual abundance ( $N_{c,t,summ}$ ) were not monitored in the first ten trials to expedite results, but population size estimates are of interest to managers as measures of population state that could be used to monitor population change and evaluate management options. Given the model's difficulty in estimating the effect of WL on alligator detection probability, latent abundance estimates may be off and/or highly uncertain. It is also possible that although the individual parameters had issues, across the ensemble of estimates (i.e., for the mean, slope, quadratic terms), prediction of detection probability given WL may be reasonable. When additional iterations are run in JAGS, all unknowns in the model that were initially excluded to reduce computation time should be monitored, including latent nest, egg, and size class abundances because the latent population is the target of management actions.

An ideal conclusion at the end of this study would be that: (1) the estimation model produced accurate and precise posterior distributions for population and observation process parameters in the alligator IPM, and (2) the model accurately and consistently predicts changes in population size and structure when parameterized with the estimation model results ensuring its forecasts can provide reliable decision guidance. It is premature to draw such conclusions at this time because the initial assessment of the IPM presented here involved only ten trials. A larger sample of trials is warranted to confirm the stability of the results. Additionally, the first ten trials, and any future trials, should run for additional iterations because MCMC chains for

some parameters have not converged, e.g.,  $\bar{\phi}_H$ . In these cases, a longer burn-in period is required. In other cases, indicators suggest the model reached convergence, but more iterations are needed to increase the effective posterior sample size (N.eff). Keeping this in mind, the results from the first ten trials are discussed.

Several assumptions need to be met for the results to be salient. First, we assume the latent population simulation model responsible for generating the population records underlying trial data sets captures the biological mechanisms responsible for alligator population dynamics. Because I programmed the demographic processes according to published alligator research, and time series generated under the model achieve stability before and after an annual harvest process is initiated, I believe the simulation model in its current form is a reasonable approximation of Orange Lake alligator population biology. However, aspects of alligator ecology that bear on population dynamics are notably missing.

For one, population processes in the simulation model are unaffected by environmental conditions. There is widespread agreement that environmental conditions influence alligator physiology, behavior, and spatial distribution at multiple scales, from local to regional. Currently, the data simulation and estimation models incorporate the effect of WL on count survey detection probability, but environmental variables, particularly WL, influence population processes as well due to the synergistic effects of changing habitat availability and population density, increased mortality from intraspecies interactions, and changes in prey availability. Water levels and flooding events affect nest production (Joanen et al., 1977; Percival et al., 1992), as well as nesting and hatchling success though the effects are spatially variable (Rice & Percival, 1995). Alligator habitat availability varies in response to changes in WL with immediate direct and longer-term indirect effects on alligator populations. With the modeling

framework presented here, WL and other abiotic covariates (e.g., water temperature) can be incorporated into demographic and observation processes in the IPM to help differentiate the impact in other parts of the model. In future simulation studies, the influence of environmental variables on population processes can be incorporated into the population simulation and estimation models.

Also, for simplicity, I assumed the simulated population was closed to movement of alligators in or out of the study system. The real Orange Lake alligator population is not completely closed to emigration and immigration due to hydrologic connectivity between Orange Lake and other water bodies in the Orange Creek drainage of north-central Florida. Movement of alligators sometimes occurs between Orange Lake and adjacent Lochloosa Lake, one of the other treatment lakes in the FFWCC's experimental harvest study (Woodward et al., 1992).

Second, we assume the simulated data fitted with the IPM is an accurate representation of real alligator data sets to be fitted in the future. Trial data sets were created to resemble real alligator data. The FFWCC's real alligator data sets are more extensive and contain more gaps (missing observations) and anomalies. For example, though several decades of alligator capture history data have been collected, initial captures in some years occurred during different months and recapture effort was inconsistent over time. The FFWCC's eyeshine count survey data also span decades, and counts are grouped into 1-ft TL increments with multiple unknown categories (e.g., unknown but > 4 ft, unknown > 6 ft). For a researcher interested in testing model sensitivity to data quantity or quality, replicate IPM data sets can be simulated with missing observations, under observation processes representing alternative hypotheses about the effects

of different researchers' biases, or any other set of circumstances that have the potential to introduce uncertainty.

An assumption required for this model to be of use to alligator managers elsewhere, i.e., to be helpful for making inferences about alligators in other parts of their range, is that the OL alligator population is representative of other alligator populations. Orange Lake may not be representative of other populations. It is unique even among other AMUs in FL. Orange Lake is among the best studied alligator populations in FL, and where data exists, such as Woodward et al. (1992), it is apparent Orange Lake differs from other lakes in several ways. For instance, the alligator population at Orange Lake is one of the densest in FL (Normandeau Associates, 2016). Also, female alligators at Orange Lake reach sexual maturity at a smaller size (TL) (Woodward et al., 1992). Differences in habitat are correlated with differences in alligator body size, condition, and growth dynamics. If any of the assumptions are violated, model performance in trials with simulated data may poorly represent the results produced when fitting the model to data from real alligator populations. In that case, validating the model through simulation as demonstrated here will have little practical value.

Sources of bias also need to be recognized. The results reported here have the potential to be derivative of one or more of the analytical decisions I made during the research process. Potential sources of selection bias include my choice for any of the latent population simulation sub-models, their functional form, or parameterizations: among these include the density-dependent relationships between annual size class-specific survival probabilities and changes in the  $ad^+$  density; logistic puberty process as a function of TL and its density-dependent relationship with the  $ad^+$  population; use of an alligator snout-vent length growth model parameterized for SC alligators and transformed to simulate changes in TL; selection of WL as a

covariate for the count survey detection probability model; and choice of a quadratic relationship between detection probability on the logit scale and WL. I also simulated the latent population through an individual-based life history model. Phenomenological population models used historically are more efficient than individual-based models. Population-level models typically run faster because they have fewer states to track. I argue, however, alligators warrant an individual-based model due to their growth dynamics and interdependencies between size and life stage. On the other hand, for managers, a faster population model provides an opportunity to develop multiple competing models from which managers can learn over time in an adaptive harvest management framework. Gains in speed make it possible to consider many different models at the same time to estimate then optimize the model used to make population predictions for decision making. If there is an advantage of learning over time in terms of differentiating among models representing different hypotheses about population biology, the tradeoff may be worth it.

My evaluation of only one of many possible specifications of an IPM for alligators is another possible source of bias. Multiple IPMs could be formulated to capture alternative hypotheses about structural relations between population processes and states as already mentioned. Without changing the system processes, the prototype IPM could be programmed (i.e., coded) differently by using different syntax, prior distributions for parameters, or MCMC chain initial values. Any of the changes can influence the efficiency of the model. The relatively small trial sample size ( $n = 10$ ) used in this initial evaluation of the IPM may also affect results given there are many possible stochastic realizations of the latent population and observation processes used to produce trial data sets.

The length of the MCMC chains containing draws from posterior distributions directly influences parameter estimates and may be a possible source of measurement bias. Measurement bias may be introduced through the model performance measures used or not used to evaluate results. My initial assessment of the model considered whether 95% BCIs contained latent parameter values. There are other ways to measure the quality of the results. Due to their complexity, IPMs elude traditional goodness-of-fit tests. However, methods such as posterior predictive checks may be conducted to see whether the model is capable of giving rise to the data (Hobbs & Hooten, 2015). This is a critical consideration in any Bayesian analysis. The calculations can be incorporated into the estimation model and Bayesian p-values can be monitored alongside unknown population parameters. Discrepancy measures can also be defined as derived quantities in the estimation model and monitored with other unknowns to gain insight regarding the model's performance.

Confounding bias, a third type of bias, exists among parameters that are unidentifiable. Parameter identifiability issues likely made it difficult to estimate  $\lambda$  and  $r_H$ . Estimates for  $\lambda$  and  $r_H$  may also be affected by the fact that the estimation model does not account for variability in annual harvest rates generated by imperfect implementation of the annual quota (i.e., partial controllability) that was built into the population simulation model. Difficulty estimating  $p_{FMN}$  in the first ten trials may be due to the absence of data related to sex ratios, the puberty process, or individuals' breeding state (Figure 3.19). Estimates of  $p_{FMN}$  may be confounded with  $\sigma_{CL}$  making both unidentifiable.

Of the demographic parameters considered in the Orange Lake harvest model developed by Rice and Percival (1995) population growth was most sensitive to changes in the proportion of females nesting (Woodward, 1996a); however, proportion of females nesting in a given year

was the only density-dependent factor included in their model. It was included because they believed it could be measured across areas (i.e., alligator management units) (Rice & Percival, 1995). As a reminder, they had set out to identify populations with similar responses to harvest so they could group AMUs with similar population dynamics and develop policies appropriate for each group.

Additional trials, longer MCMC chains, and estimating posterior distributions for a greater number of variables, including latent states and discrepancy measures, will provide a more complete understanding of the IPM's behavior, but it may be time consuming under the current design. In its present form, the estimation model is inefficient, and slow computations caused by inefficient MCMC algorithms are compounded in simulation studies, such as this, which need to run many times (Monnahan et al., 2017). Consequently, there is a tradeoff between reducing uncertainty and having an answer quickly.

Analytical performance may be improved by using a different family of MCMC search algorithms to estimate posterior distributions. In JAGS, many of the algorithms use inefficient random-walk behavior that undermines their performance (Monnahan et al., 2017). Hamiltonian Monte Carlo (HMC) algorithms, in contrast, make directed MCMC transitions using posterior geometry and properties of Hamiltonian dynamics, resulting in greater efficiency and faster inferences (Monnahan et al., 2017). Though not without their own limitations, e.g., an inability to accommodate discrete parameters such as individual latent states, HMC algorithms are increasingly being used by ecologists through flexible software platforms, such as Stan and Nimble (Dail & Madsen, 2011; Monnahan et al., 2017).

The alligator population at the Orange Lake AMU in Florida provided a model system for validating an IPM for alligators. Future work should fit the IPM to real Orange Lake data

because its purpose is to help agencies, most immediately the FFWCC, make inferences about real alligator populations. A longer-term view of model development and testing includes incorporating density-dependence into the estimation model and incorporating information about sex ratios. The latter can inform estimates for  $p_{FMN}$ . The local-scale model may eventually be scaled up to account for spatially structured population dynamics at more regional scales as well. Implementing the alligator IPM within a decision framework will help to establish a direct link between data and decision making that should allow managers to base harvest management decisions on population state and scientific understanding of how it will likely change in the future, accounting for uncertainty.

Table 3.1

*Initial Population Simulation Parameters*

Size class	Index ( <i>c</i> )	TL range (cm)	$N_{0c}$	$\rho_{Fc}$
Hatchling	H (1)	[0, 30)	658	0.50 <sup>b</sup>
Juvenile	J (2)	[30, 122)	4100 <sup>a</sup>	0.37 <sup>c</sup>
Subadults	SA (3)	[122, 183)	950 <sup>a</sup>	0.47 <sup>c</sup>
Adults	A (4)	[183, 274)	1080 <sup>a</sup>	0.47 <sup>c</sup>
Bulls	B (5)	[274, 390)	720	0.01 <sup>b</sup>

*Note:* Size class (*c*) thresholds delimited by alligator total length (TL, cm); initial distribution of population members among size classes ( $N_{0c}$ ), and probability of being female ( $\rho_{Fc}$ ) used in binomial sex assignment process for initial population members.

<sup>a</sup> Estimates for alligators at OL 1981-1987 (Delany et al., 2011)

<sup>b</sup> Hypothetical

<sup>c</sup> Woodward (1996a)

Table 3.2

*Density-Dependent Survival Process Parameters*

Size class ( <i>c</i> )	$\phi_{0c}$ <sup>a</sup>	$\Delta\phi_{0c}$	$b_c$
Hatchling (H)	0.411 <sup>b</sup>	$\pm 0.08$	-1.42723
Juvenile (J)	0.843	$\pm 0.06$	-2.02444
Subadults (SA)	0.8552	$\pm 0.10$	-4.12924
Adults (A)	0.9057	$\pm 0.10$ <sup>c</sup>	-11.7154
Bulls (B)	0.8234	$\pm 0.10$	-3.26396

*Note:* Baseline size-specific annual survival probability in the absence of harvest ( $\phi_{0c}$ ); range of deviation from baseline survival rates ( $\Delta\phi_{0c}$ ) and slope ( $b_c$ ) for linear model on the logit scale relating changes in survival to deviations in density of the adult<sup>+</sup> population from an intermediary level.

<sup>a</sup> Rice and Percival (1995)

<sup>b</sup> Woodward et al. (1987)

<sup>c</sup> upper limit  $\phi_{0A} = 1$

Table 3.3

*Sex-Specific Alligator Growth Model Parameters*

Parameter	Sex	
	Female	Male
$a_s$	0.11	0.09
$b_s$	0.72	0.69
$\Delta$	1	
$\tau_1$	0	
$\tau_2$	45	
$y_1$	12.5	
$y_{2,s}$	135.9	186.9
$\epsilon_s^a$	5.9	7.42

*Note:* Except where noted, values from Wilkinson et al. (2016), including sex-specific rate ( $a_s$ ) and shape ( $b_s$ ), terminal snout-vent length ( $y_{2,s}$  cm), and model error ( $\epsilon_s$ ). The same values were used for both sexes for the duration of the growth period ( $\Delta$ , years), standard snout-vent length at hatching ( $y_1$ , cm), standard age at hatching ( $\tau_1$ , years), and maximum life expectancy ( $\tau_2$ , years).

<sup>a</sup> Estimated through simulation based on Wilkinson et al. (2016).

Table 3.4

*Initial Capture Sample Sizes for Mark-Recapture-Recovery Data*

Size Class	Year ( $t$ )										
	1	2	3	4	5	6	7	8	9	10	11
Hatchlings	1	1	9	2	12	17	0	2	1	0	0
Juveniles	73	117	168	159	61	43	5	7	18	11	0
Subadults	7	34	2	2	1	0	0	0	0	2	23
Adults	1	6	0	0	0	0	0	0	2	9	5
Bulls	0	1	0	0	0	0	0	0	2	5	6

*Note:* Sample sizes of marked alligators initially captured and released by the FWC at the Orange Lake Alligator Management Unit (AMU 722) between April 15 – July 14, 1980 – 1989, by size class, used as the basis for generating simulated mark-recapture-recovery data sets.

Table 3.5

*Size Class-Specific Recapture Probabilities in MRR Data Simulation Model*

Size class ( $c$ )	$p_c$
Hatchling (1)	0.623 <sup>a</sup>
Juvenile (2)	0.230 <sup>b</sup>
Subadult (3)	0.180 <sup>c</sup>
Adult (4)	0.130 <sup>c</sup>
Bull (5)	0.080 <sup>c</sup>

*Note:* Annual state-specific recapture probabilities ( $p_c$ ) for simulated marked and released individuals. Marked individuals in subadult, adult, or bull size classes harvested in  $t$  were recovered in states 6, 7, or 8, respectively, in  $(t + 1)$  with probability equal to 1.

<sup>a</sup> Mean estimated inter-cohort hatchling detection probabilities for spring  $(t + 1)$  (0.72, 0.30, 0.85) (Woodward et al., 1987)

<sup>b</sup> Mean estimated inter-cohort hatchling detection probabilities for spring  $(t + 2)$  (0.24, 0.29, 0.16) (Woodward et al., 1987)

<sup>c</sup> Hypothetical values computed by subtracting 0.05 from the preceding size class ( $p_{(c-1)}$ )

Table 3.6

*Count Survey Observation Model Parameters*

Size class ( $c$ )	$\beta_{1c}$	$\beta_{2c}$	$\beta_{3c}$
Hatchling (1)	-0.75	-0.8	0.00091
Juvenile (2)	-0.8	-0.8	0.00090
Subadult (3)	-1.7	-0.6	0.00050
Adult <sup>+</sup> (4 & 5)	-1.9	-0.5	0.00010

*Note:* Count survey observation process parameters used in the data simulation model to specify a quadratic relationship between water level and detection probability on the logit scale for each size class:  $\text{logit}(p_{C_{c,t,j}}) = \beta_{1,c} + \beta_{2,c} \text{cWL}_{t,j} + \beta_{3,c} \text{cWL}_{t,j}^2$

Table 3.7

*Estimation Model Prior Distributions*

Parameter	Prior distribution
$N_{0c}$	U(2000, 30000)
$\lambda$	U(0, 0.5)
$\Psi_c$	U(0, 1)
$\bar{\phi}_c$	U(0, 1)
$\sigma_{\bar{\phi}_c}$	U(0, 1)
$\phi_{egg}$	U(0, 1)
$p_c$	U(0, 1)
$\Gamma_H$	U(0.5, 1)
$\mu_{CL}$	U(30, 40)
$\sigma_{\mu_{CL}}$	U(0, 10)
$p_{CL}$	U(0, 1)
$p_{FMN}$	U(0, 1)
$\beta_{1:3c}$	N(0, 0.37)

*Note:* Uniform (U) and Normal (N) distributions abbreviated.

Table 3.8

*Latent Values for Population System and Observation Process Parameters*

Parameter	Size Class ( <i>c</i> )				
	Hatchling (H)	Juvenile (J)	Subadult (SA)	Adult (A)	Bull (B)
$\bar{\phi}_c$	0.4461 (0.003)	0.8682 (0.002)	0.8986 (0.003)	0.9628 (0.003)	0.8655 (0.003)
$\sigma_{\bar{\phi}_c}$	0.0189 (0.002)	0.0130 (0.001)	0.0221 (0.002)	0.0289 (0.003)	0.0218 (0.002)
$\psi_c$	0.977 (0.001)	0.145 (0.001)	0.150 (0.004)	0.0376 (0.002)	
$p_c$	0.62	0.23	0.18	0.13	0.08
$\beta_{1c}$	-0.75	-0.80	-1.70	-1.90	-1.90
$\beta_{2c}$	-0.80	-0.80	-0.60	-0.50	-0.50
$\beta_{3c}$	0.00091	0.00090	0.00050	0.00010	0.00010
$\lambda$				0.13	
$r_H$				0.90	
$\mu_{CL}$					33
$\sigma_{CL}$					5.80 (0.174)
$\rho_{FMN}$					0.153 (0.006)

*Note:* Parameter values specified *a priori* are presented as single values. Parameters that emerge through interactions between system state and processes in the context of simulations are presented as the mean and SD computed from the latent population records simulated for each replicate IPM data set ( $n = 10$ ) during the study period ( $t_{H0}:t_{H0} + 10$ ).

Table 3.9

*JAGS MCMC Posterior Sample Statistics*

Parameter	Mean $\widehat{R}$ (SD)	Mean N.eff (SD)	Proportion of trials where 95% BCI contains latent value
$\beta_{1,H}$	1.06 (0.0771)	681 (1327)	0.1
$\beta_{1,J}$	1.01 (0.0122)	477 (517)	1
$\beta_{1,SA}$	1.12 (0.108)	147 (348)	0
$\beta_{1,A}$	1.14 (0.137)	62.6 (62.5)	0
$\beta_{1,B}$	1.14 (0.137)	62.6 (62.5)	0
$\beta_{2,H}$	1.05 (0.0593)	391 (623)	0.2
$\beta_{2,J}$	1.01 (0.00608)	431 (371)	1
$\beta_{2,SA}$	1.01 (0.00866)	452 (400)	0.2
$\beta_{2,A}$	1.01 (0.00637)	1360 (1716)	0.8
$\beta_{2,B}$	1.01 (0.00637)	1360 (1716)	0.8
$\beta_{3,H}$	1.03 (0.0458)	739 (1367)	0.3
$\beta_{3,J}$	1.01 (0.00414)	604 (445)	0.9
$\beta_{3,SA}$	1.01 (0.0106)	696 (802)	0.3
$\beta_{3,A}$	1.01 (0.00403)	1859 (2890)	0.5
$\beta_{3,B}$	1.01 (0.00403)	1859 (2890)	0.5
$\mu_{CL}$	1.00 (0.000201)	19830 (15404)	1
$\sigma_{\mu_{CL}}$	1.00 (0.000724)	17684 (31950)	0
$\lambda$	1.06 (0.0578)	404 (953)	0.1
$\bar{\Phi}_H$	1.12 (0.108)	52.8 (49.7)	0.4
$\bar{\Phi}_J$	1.03 (0.0369)	600 (797)	0.8
$\bar{\Phi}_{SA}$	1.00 (0.00602)	32827 (93953)	1
$\bar{\Phi}_A$	1.01 (0.00382)	1747 (2363)	1

Parameter	Mean $\widehat{R}$ (SD)	Mean N.eff (SD)	Proportion of trials where 95% BCI contains latent value
$\bar{\Phi}_B$	1.00 (0.00286)	3442 (5783)	1
$\phi_{\text{egg}}$	1.17 (0.142)	109 (260)	0.9
$p_H$	1.01 (0.00835)	7271 (20096)	1
$p_J$	1.02 (0.0161)	252 (236)	1
$p_{SA}$	1.03 (0.0267)	2055 (5854)	1
$p_A$	1.00 (0.00121)	43099 (94563)	1
$p_B$	1.00 (0.0000503)	166834 (125386)	1
$p_{CL}$	1.08 (0.0919)	363 (739)	0.9
$p_{FMN}$	1.18 (0.185)	153 (172)	0.3
$\Psi_H$	1.05 (0.0498)	1015 (2022)	0.8
$\Psi_J$	1.05 (0.0586)	156 (203)	0
$\Psi_{SA}$	1.03 (0.0278)	1148 (2338)	0.7
$\Psi_A$	1.01 (0.00875)	5531 (15797)	1
$r_H$	1.06 (0.0401)	97.2 (96.1)	0
$\sigma_{\bar{\Phi}_H}$	1.03 (0.0295)	899 (1596)	1
$\sigma_{\bar{\Phi}_J}$	1.01 (0.00728)	2142 (2367)	1
$\sigma_{\bar{\Phi}_{SA}}$	1.00 (0.000755)	2415 (987)	0.2
$\sigma_{\bar{\Phi}_A}$	1.01 (0.00346)	2461 (3605)	1
$\sigma_{\bar{\Phi}_B}$	1.00 (0.00572)	3002 (3195)	1

Table 3.10

## Chapter 3 Notation

Abbreviations and Indices		
Term	Description	Value
$A_{OL}$	area of Orange Lake, Florida (ha)	5251.5
TL	total length; distance between alligator's snout and vent in cm	
SVL	snout-vent length; distance between alligator's snout and vent (cm)	
$sa^+$	alligators $\geq 122$ cm TL, including subadult, adult, and bull sizes classes ( $c = 3, 4,$ and $5$ ); subject to harvest mortality during hunting season; harvestable	
$ad^+$	alligators $\geq 183$ cm TL, including adult and bull sizes classes ( $c = 4$ and $5$ )	
subadult <sup>+</sup>	alligators $\geq 122$ cm TL, including subadult, adult, and bull sizes classes ( $c \ni 3, 4,$ and $5,$ respectively); harvestable	
adult <sup>+</sup>	alligators $\geq 183$ cm TL, including adult and bull sizes classes ( $c \ni 4$ and $5$ )	
$t$	year index	
$i$	individual alligator index	
$s$	sex; 1 = female, 2 = male	
$c$	size class index; 1 = hatchling, 2 = juvenile, 3 = subadult, 4 = adult, 5 = bull	
$hc$	harvest class index; 1 = sub-adult ( $c = 3$ ), 2 = adult ( $c = 4$ ), 3 = bull ( $c = 5$ )	
$z$	latent individual state index; 1:5 = alive in size class $c$ , 6:8 = recently harvested from size class 3:5, respectively, and 9 = dead	
$k$	capture history segment index; in marginalized MRR likelihood	

Initial Population		
Term	Description	Value
$t_{H0}$	first year of harvest	51
$\rho F_c$	estimated proportion of females in each size class, used to assign sex to founding population members and hatchling recruits joining the population each fall	Table 3.1
Individual Covariates		
Term	Description	Value
$sex_i$	sex of alligator $i$ , 1 = female, 2 = male	
$age_i$	number of years since individual $i$ was recruited into the population as a hatchling	
$TL_{i,t}$	total length (TL) of individual $i$ in summer $t$ in cm	
$\phi_{i,t}$	annual probability survival outside of hunting season for individual $i$ in year $t$ ; equal to $\phi_{c,t}$ unless $age_i \geq 40$ , then $\phi_{i,t}$ is a function of $age_i$ ,	
$s_{i,t}$	outcome of annual survival outside hunting season for individual $i$ in year $t$	
$\rho_{Mi,t}$	probability adult female $i$ reaches sexual maturity in year	
$SVL_{i,t}$	snout-vent length (cm) of individual $i$ at time $t$	
$SVL_{i,(t+1)}$	realized snout-vent length (cm) for individual $i$ at $t+1$ from growth model	
$\delta_{i,t}$	size of individual $i$ in year $t$ after annual growth process; equivalent to $TL_{i,(t+1)}$	
$Z_{i,t}$	latent state for individual $i$ in year $t$	

Total Length Growth Model		
Term	Description	Value
$\alpha_s$	sex-specific intercept in alligator SVL-to-TL (cm) conversion	2.2390 (F) 2.3121 (M)
$\beta_s$	sex-specific power coefficient in alligator SVL-to-TL (cm) conversion	0.9707 (F) 0.9622 (M)
$a_s$	sex-specific rate parameter for growth model	0.11 (F) 0.09 (M)
$b_s$	sex-specific shape parameter for growth model	0.72 (F) 0.69 (M)
$\tau_1$	standard age at hatching (years)	0
$\tau_2$	life expectancy (years)	45
$\Delta$	duration of growth period (years)	1
$y_1$	standard snout-vent length at hatching (cm)	12.5
$y_{2,s}$	sex-specific terminal snout-vent length (cm)	135.9 (F) 186.9 (M)
$\epsilon_s$	estimated sex-specific growth model error term	5.9 (F) 7.42 (M)
$SVL_{i,t}$	snout-vent length (cm) for individual $i$ at time $t$	
$SVL_i^0$	expected snout-vent length (cm) for individual $i$ at $t+1$ from growth model	
$SVL_{i,(t+1)}^0$	realized SVL (cm) at $t+1$ for individuals that are still growing	
$SVL_{i,(t+1)}$	SVL (cm) at $t+1$ for individuals that are still growing	
Harvest Process Parameters		
Term	Description	Value
$\lambda$	annual harvest rate for subadult <sup>+</sup> alligators, $\geq 122$ cm TL; specified as the harvest probability (0.13) in the binomial harvest model used in the latent population simulation model	0.13 or 13%
$H_t$	latent total realized number of alligators harvested during hunting season in year $t$	
$H_{hc,t}$	number of alligators in harvest class $hc$ removed from the population through hunter harvest in year $t$	
$H_{ad+,t}$	number of hunter-harvested alligators $\geq 183$ cm TL in $t$	

Survival Process Parameters		
Term	Description	Value
$\phi_{0c}$	expected survival probability for size class $c$ when $D_{ad+}$ equals $D_0$ , an intermediate between $D_{c,max}$ and $D_{c,min}$ ; baseline annual probability of survival in the absence of density dependence for individuals in size class $c$	Table 3.2
$\phi_{c,max}$	upper limit for density-dependent response in survival probability for alligators in size class $c$ ; used to derive $b_c$	Table 3.2
$\phi_{c,min}$	lower bound for size class $c$ survival probability ( $\phi_{c,t}$ ) used to derive $b_c$	Table 3.2
$\phi_{c,t}$	density-dependent survival probability for alligators in size class $c$ for the remainder of year $t$ after hunting season;  $\text{logit}(\phi_{c,t}) = \text{logit}(\phi_{0c}) + b_c (\log_{10}(D_{ad+,t,postH}) - \log_{10}(D_0))$	
Latent Abundances and Densities		
Term	Description	Value
$N_{c,t,summ}$	abundance of size class $c$ in summer of year $t$	
$N_{sa+}$	abundance of the subadult <sup>+</sup> population; $\geq 122$ cm TL	
$N_{ad+}$	abundance of the adult <sup>+</sup> population; $\geq 183$ cm TL	
$N_{ad+,t,fall}$	abundance of the adult <sup>+</sup> population at the beginning of hunting season, before harvest in year $t$	
$N_{ad+,t,postH}$	abundance of the adult <sup>+</sup> population after hunting season in year $t$	
$D_t$	number of adult <sup>+</sup> in the fall after harvest in years $t \geq t_{H0}$ , or directly after recruitment in earlier years, divided by the area of Orange Lake ( $A_{OL}$ )	
$D_{ad+}$	density of adult <sup>+</sup> population; $N_{ad+} / A_{OL}$	
$D_{ad+,t,postH}$	density of alligators $\geq 183$ cm TL after hunting season in $t$ ; $N_{ad+,t} - H_{ad+,t}$	
$D_{ad+,t}$	density of alligators $\geq 183$ cm TL at the beginning of the hunting season in $t$	
$D_0$	intermediate adult <sup>+</sup> population density used as reference point for density-dependent processes	0.193

$D_{max}$	lower bound for adult <sup>+</sup> population density used to derive the slope parameter for the density-dependent survival function, $b_c$ ; based on the minimum adult <sup>+</sup> population size estimate for OL during the FFWCC's experimental harvest study (1981 - 1990), which was 514.3 adult+ alligators in 1990 (Woodward et al., 1992)	0.098
$D_{min}$	upper bound for adult <sup>+</sup> population density used to derive the slope parameter for the density-dependent survival function, $b_c$ ; based on the maximum adult+ population size estimate for OL during the FFWCC's experimental harvest study (1981 - 1990), which was 1513.4 adult+ alligators in 1990 (Woodward et al., 1992)	0.288
$TL_0$	TL size (cm) at which probability that a female becomes mature 0.5	200.4529
$TL_D$	density-dependent adjustment to $TL_0$ in female puberty process model	

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Density-Dependent Process Parameters

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Term	Description	Value
$b_c$	size class-specific slope parameter relating survival probability on the logit scale to adult <sup>+</sup> density	Table 3.2
$b_D$	slope in density-dependent puberty process that shifts the relationship between an immature adult female alligator's $TL_{i,t}$ and her probability of reaching maturity $\rho_{Mi}$ before annual nesting begins for summer $t$ based on deviations in $D_{ad+}$ from $D_0$ on the log scale	39.622
$b_{OL}$	slope of linear puberty process model on the logit scale	0.08713

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Latent Reproduction Parameters

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Term	Description	Value
$\rho_M$	probability that an adult female reaches sexually maturity	
$\rho_{nest}$	annual probability that a mature adult female nests (Woodward et al., 1992)	0.398
$\phi_{nest}$	probability of nest survival based on the estimated mean nest survival rate at Orange Lake for the experimental harvest mean year 1985.5 (Woodward et al., 1992)	0.452
CL	expected clutch size, i.e. expected number of eggs per nest, based on the average (of annual median values for 1982 - 1990) estimated mean clutch size for Orange Lake for median year 1985.5, 32.8 (Woodward et al., 1992)	33
$\phi_{egg}$	probability that an egg will produce a viable hatchling	0.875

$N_{FM,t}$	number of sexually mature female alligators in summer $t$ after puberty process
$N_{Fn,t}$	total number of nesting adult females in the population in year $t$
$N_{nests,t}$	number of surviving nests, a subset of $N_{Fn,t}$
$N_{eggs,t}$	total number of viable eggs produced by the population in $t$ , which is a function of the number of eggs laid by nesting females and probability of nest survival total number of eggs laid by nesting females ( $N_{Fn,t}$ ) in year $t$
$N_{recruits,t}$	number of surviving eggs from nests in $t$ that are recruited into the population as hatchlings at the beginning of year $t + 1$

MRR Data Simulation and Likelihood		
Term	Description	Value
$p_c$	size-specific recapture probabilities used to generate alligator capture histories for latent population members, Table 3.5; probability marked alligator in size class $c$ is recaptured alive, unknown variable (parameter) in the estimation model (Table 3.7)	
$z_{obs,i,t}$	state observed for individual $i$ in summer $t$	
$rrCH_{k,t}$	Observed state in year $t$ in capture history segment $k$ ; marginalized MRR data likelihood	
$N_{\pi CH}$	total number of unique capture history segments, $k \in [1, N_{\pi CH}]$ ; marginalized MRR data likelihood	
$rrFR_k$	frequency of capture history segment $k$ in the MRR data; marginalized MRR data likelihood	
$first_k$	latent state at release occasion for capture history segment $k$	
$last_k$	latent state at recapture or recovery occasion for capture history segment $k$	
$\mathbf{tr}$	three-dimensional array $(k, t, z)$ specifying annual latent state transitions; for capture segment $rrCH_k$ based on latent state $(z)$ at time $t$ (for $t = (first_k+1)$ through $(last_k-1)$ ), the vector $\mathbf{tr}_{k,t,1:9}$ specifies the probability that $z_{(t+1)}$ equals $z$ given $z_t$ , for $t = 1:(T-1)$ and $z = 1:9$	Figure 3.8
$\phi_{c,t}$	survival probability for size class $c$ in year $t$	
$\psi_c$	transition probability for alligators in size class $c$ for alligators $< 274$ cm TL	
$\lambda$	harvest probability for subadult <sup>+</sup> alligators during hunting season	

MRR Data Simulation and Likelihood, *continued*

Term	Description	Value
<b>rho</b>	three-dimensional observation process array; for each latent state $z$ at time $t$ , $\mathbf{rho}_{z,t,1:9}$ is a vector of values corresponding to the probability of being observed in state $z$ at $t$ given latent state $z_t$ , for $t = 1:(T - 1)$ and $z = 1:9$	Figure 3.8
<b>pz</b>	array with dimensions $k, t, z$ that integrates state transition ( <b>tr</b> ) and recapture ( <b>rho</b> ) probabilities over time based on $Z_{obs,firstk}$ and $Z_{obs,lastk}$ , and the number of occasions ( $t$ ) elapsed between $first_k$ and $last_k$ ; used to calculate the likelihood of capture segment $k$ ; rows correspond to capture segments ( $k$ ), populated on occasion $t = first_k$ with a 1 assigned to $z = Z_{obs,firstk}$ and 0 to all other levels of $z$ at $t = first_k$ ; thereafter, $pZ_{k,(t+1),1:9}$ for $t = first_k:(last_k - 1)$ , is populated with the likelihood of being in each state $z$ by the product of (a) the matrix multiplication product of $pZ_{k,t,1:9}$ and $\mathbf{tr}_{1:9,t,z}$ , and (b) the probability of being observed in each state ( $\mathbf{rho}_{z,t,rrCHK_{-(t+1)}}$ ); the probability of latent state $z$ when $t = last_k$ is then computed by summing the probabilities over all states.	
$pZ_{k,last_{[k]},z}$	probability the last observed state is $z$ given latent state at $t = last_k$	
$lik_k$	cumulative likelihood for capture segment $rrCH_k$ ; in marginalized MRR data likelihood	
$one_k$	scaled probability of the likelihood for capture segment $rrCH_k$ ; using variation of the JAGS "ones trick," $lik_k$ is sampled from a binomial distribution based on its frequency ( $rrFR_k$ ) among individual capture histories in the MRR data set, $\sim \text{Binomial}(rrFR_k, lik_k)$ in the marginalized MRR data likelihood	

Count Survey Data Simulation and Likelihood

Term	Description	Value
$\mu_{WLOL}$	mean average monthly water level at Orange Lake, FL for months June, July, August, and September, 1980-1991 (U.S. Geological Survey, 2016)	57.09402
$\sigma_{\mu_{WLOL}}$	standard deviation of the average monthly water level at Orange Lake, FL for months June, July, August, and September, 1980-1991	1.512709
$WL_{t,1}$	randomly simulated water level covariate data for the first replicate ( $j = 1$ ) count survey each year $t$ ; used in data simulation model	

$WL_{t,2}$	randomly simulated water level covariate data for the second replicate ( $j = 2$ ) count survey each year $t$ ; used in data simulation model	
$WL_{t,j}$	water level observation associated with annual count survey replicate $j$ in year $t$	
$\overline{WL}$	average count survey water level (ft), i.e. average $WL_{t,j}$ for all years, $t = 1:T$ , and survey replicates, $j = 1:2$	56.905
cWL	centered water level count survey covariate data	
cWL $_{t,j}$	water level observation associated with annual count survey replicate $j$ in year $t$	
$\beta_{1:3,c}$	size class-specific coefficients for quadratic count survey detection probability model on logit scale used to simulate annual count data	Table 3.6
$pC_{c,t,j}$	size-specific detection probability for alligators in size class $c$ during annual count survey replicate $j$ in year $t$	
$Y_{c,t,j}$	count survey data - number of alligators in size class $c$ counted in year $t$ during survey replicate $j$ - simulated from a binomial distribution, $\sim \text{Binomial}(N_{c,t,summ}, pC_{c,t,j})$ , for replicate IPM data sets	

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Nesting Data Simulation and Likelihood

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Term	Description	Value
$p_{CL}$	probability of observing a clutch, or nest detection probability, used to simulate nesting data sets for IPM; an unknown variable (parameter) in the estimation model (Table 3.7)	0.94
$N_{\text{eggs},Rt,i}$	number of eggs counted in nest $i$ year $t$	
$R_t$	total number of nests observed in summer $t$ ; nesting data	
$J_t$	total number of eggs observed in nests in summer $t$ ; nesting data	

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Harvest Data Simulation and Likelihood

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Term	Description	Value
$r_H$	hunter harvest report rate used to simulate harvest data from latent harvest records for IPM data sets, equals 0.90; unknown variable (parameter) in the estimation model (Table 3.7)	0.9
$yH_{hc,t}$	number of alligators in harvest size class $hc$ reported as harvested in year $t$ ; annual harvest data likelihood	

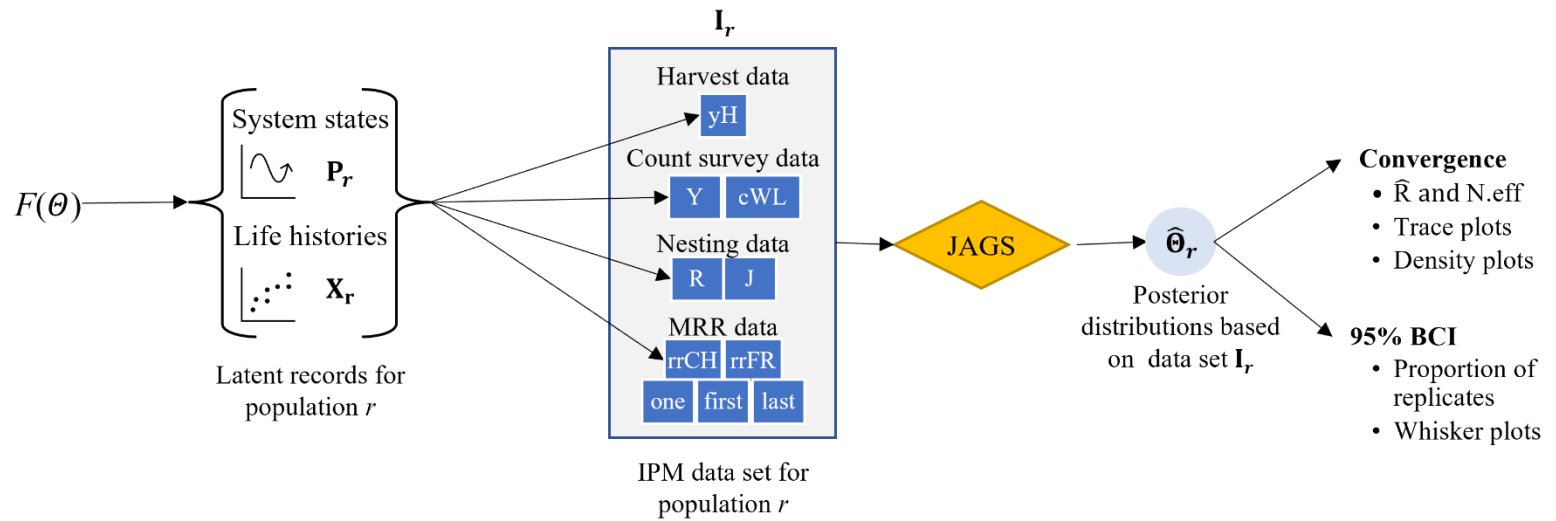
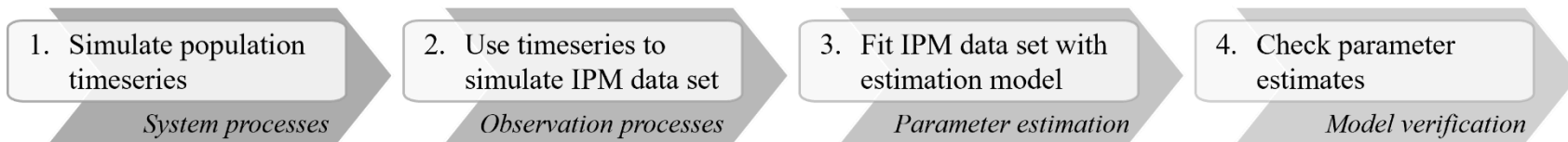
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Other Estimation Model Terms

Term	Description	Value
$pN_{0c}$	size class distribution at $t = 1$ in JAGS IPM estimation model, computed from initial size class abundances ( $N_{0c}$ ) used in the population simulation model (Table 3.1)	0.091 (H), 0.544 (J), 0.126 (SA), 0.143 (A), 0.096 (B)
$N_{0c}$	latent size class abundances at the beginning of the estimation model, for $t = 1$ (Table 3.7)	
$N_{z,t,summ}$	latent state abundances in summer $t$	
$p_{FMN}$	proportion of the latent adult <sup>+</sup> population composed of mature adult females that are nesting; unknown variable (parameter) in the estimation model (Table 3.7)	
$N_{tr,c,t}$	number of alligators in size class $c$ during summer $t$ that transition to $c + 1$ for fall $t$ , for $c \leq 4$ ; unknown state-space variable (parameter) in the estimation model	
$N_{z,t,fall}$	number of alligators in latent state $z$ at the beginning of fall $t$ , for $z = 1, 2, \dots, 9$ ; unknown state-space variable (parameter) in the estimation model	
$N_{z,t,postH}$	number of alligators in latent state $z$ after removal of individuals harvested from the population during hunting season	
$\bar{\phi}_c$	mean annual survival probability for size class $c$ , used as the expected value in the normal prior distribution for $\phi_{c,t}$ , (survival probability for size class $c$ in year $t$ )	
$\sigma_{\bar{\phi}_c}$	standard deviation for annual size class-specific survival probabilities used in the normal prior distribution for $\phi_{c,t}$ , (survival probability for size class $c$ in year $t$ )	
$\phi_{egg}$	egg survival probability; probability an egg produces a recruit for the hatchling size class in fall	
$\mu_{CL}$	expected value in normal prior distribution for mean annual clutch size ( $CL_t$ )	
$\sigma_{\mu_{CL}}$	standard deviation of the normal prior distribution for mean annual clutch size ( $CL_t$ )	

*Figure 3.1* Schematic of Chapter Workflow

Stages of the alligator IPM validation process: 1. An alligator population simulation model specifying system processes and latent parameter values ( $F(\Theta)$ ) generates one stochastic realization of the alligator population ( $r$ ) described by latent time series records for individuals ( $\mathbf{X}_r$ , e.g., change in size over time) and population-level summaries of system states ( $\mathbf{P}_r$ , e.g., change in size class abundances over time). 2. Based on the latent population records,  $\mathbf{P}_r$  and  $\mathbf{X}_r$ , and a set of observation process models, four types of demographic data are generated, which together constitute an IPM data set ( $\mathbf{I}_r$ ). 3. The data in  $\mathbf{I}_r$  are fitted with the alligator IPM through the program JAGS, which uses Bayesian inference to generate posterior distributions (estimates;  $\hat{\Theta}_r$ ) for latent population and observation process parameters. 4. Model results are checked for convergence and parameter posterior distributions are compared to known (latent) parameter values to verify the model performs as expected.



### Figure 3.2 Individual Life-Cycle Diagram

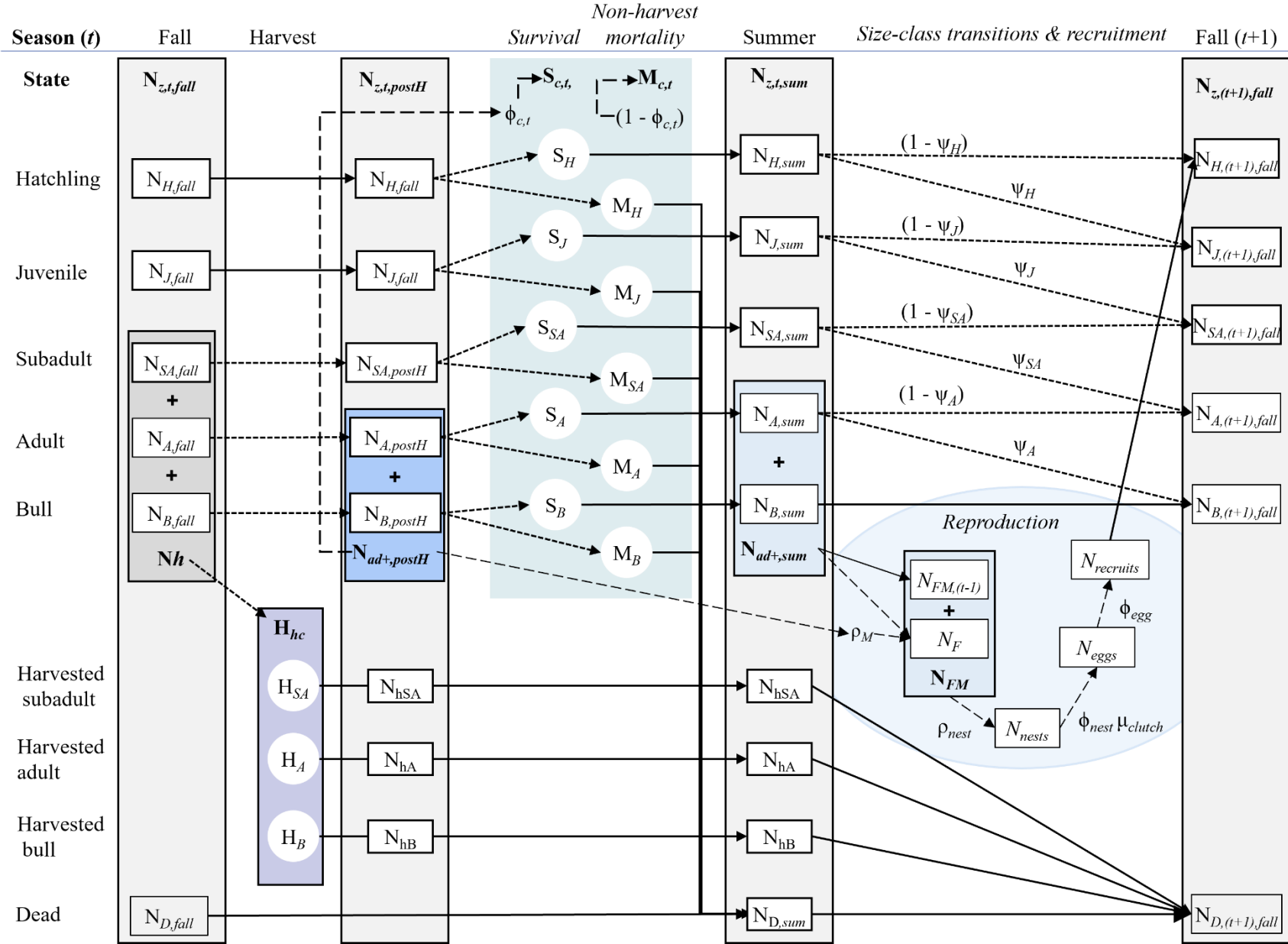
Life cycle diagram depicting annual demographic processes governing state transitions for individual simulated alligators. Seasons within the year ( $t$ ) are labeled at the top of the figure. Below them, individual state variables are printed in bold. The boxes outlining *Fall* and *Summer* contain the individual latent state ( $z$ ) at the beginning of the season. In the shaded boxes outlining *Harvest*, *Survival*, and *Growth*, the top value in bold indicates the name of the indicator variable describing individual outcomes for the associated demographic process, and the parameter(s) of the associated process are printed below in:  $f(\cdot)$ . The annual cycle begins in *Fall*,  $t$ . In years with harvest, the hunting season subjects alligators  $\geq 122$  cm TL (subadults and larger) to harvest mortality ( $h_{i,t} \sim \text{Bernoulli}(\lambda)$ ). Harvested individuals ( $h_{i,t} = 1$ ) in size classes  $c = 3, 4,$  and  $5$ , are removed from the population into the size-specific latent states  $z = 6, 7,$  and  $8$  (recently harvested subadult, adult, bull). They remain in that state until summer, thereafter they are in state  $9$  (dead). Individuals who survive the hunting season ( $h_{i,t} = 0$ ), are subject to annual survival outside of hunting season ( $s_{i,t} \sim \text{Bern}(\phi_{c_i,t})$ ). Individuals removed from the population by non-harvest mortality ( $s_{i,t} = 0$ ) are dead ( $z = 9$ ) for the remainder of the time series. Survivors ( $s_{i,t} = 1$ ) continue on to summer. During summer, the remaining population members ( $z \leq 5$ ) experience growth ( $\delta_{i,t}$ ) (a change in TL) based on a sex-specific growth model. For some individuals, growth results in a transition to the next size class for the beginning of next year (*Fall*,  $t + 1$ ).

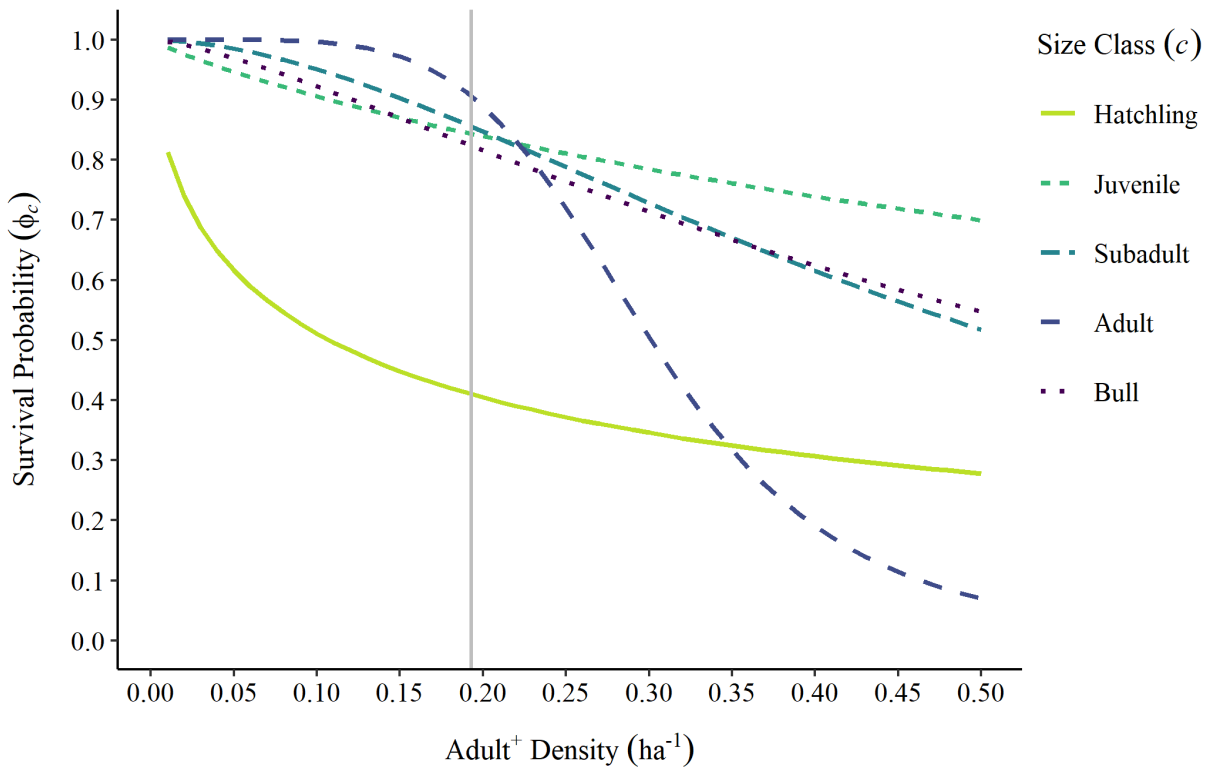


### Figure 3.3 Population State Transitions

Annual system state transitions for simulated alligator population. Population dynamics emerging from individual life histories (Figure 3.2) are summarized by latent individual states ( $z$ ; rows) and seasonal demographic processes (columns) in the annual cycle. Seasons within the year ( $t$ ) are labeled at the top of the figure;  $t$  subscripts associated with population states and process parameters have been omitted. Below the seasons, individual state variables are printed in bold. The annual cycle begins in *Fall*,  $t$ , where population members are distributed among latent states  $z = 1:5$  or 9. In years with harvest, harvestable size classes,  $N_{h,t}$ , are subject to harvest mortality. The result is some number of harvested alligators removed from harvestable size classes,  $H_{hc,t}$ . After losses from harvest, size-specific survival probabilities,  $\phi_{c,t}$ , for the remainder of the year are computed based on the reduced abundance of adult<sup>+</sup> alligators,  $N_{ad+,t,postH}$ , which is converted to adult<sup>+</sup> density ( $D_{ad+,t,sum}$ ) and fed into the density-dependent survival function. Population members in each size class are then subject to the annual survival process, which determines how many population members survive to summer ( $S_{c,t}$ ;  $N_{1:5,t,sum}$ ) versus how many are removed from the population due to non-harvest sources of mortality ( $N_{c,t,postH} - S_{c,t} = M_{c,t}$ ;  $N_{9,t,sum}$ ). In summer  $t$ , individuals harvested in  $t$  from size classes  $c = 3, 4$ , and 5, enter latent states  $z = 6, 7$ , and 8 corresponding to recently harvested subadults (hSA), adults (hA), and bulls (hB). Reproductive activities occur in summer before growth size-class transitions. The number of nests produced in summer  $t$  ( $N_{nests,t}$ ) by surviving mature adult females ( $N_{FM,t}$ ) is a function of nesting probability,  $\rho_{nest}$ .  $N_{FM,t}$  includes females that finished puberty in a previous year,  $N_{FM,(t-1)}$ , and previously immature adult females ( $N_{F,t}$ ) that reach sexual maturity at the beginning of the reproductive cycle with probability  $\rho_M$ . The probability of completing puberty,  $\rho_M$ , varies by female size ( $TL_{i,t}$ ) and the density of adult and bull alligators ( $D_{ad+,t,postH}$ ) computed from post-harvest adult<sup>+</sup> abundance ( $N_{ad+,t,postH}$ ). Nest survival probability ( $\phi_{nest}$ ) and mean clutch size ( $\mu_{clutch}$ , i.e. expected number of eggs per nest) determines how many viable eggs are produced ( $N_{eggs,t}$ ). Egg survival probability ( $\phi_{egg}$ ) then determines the number of eggs that successfully hatch from surviving clutches ( $N_{recruits,t}$ ) to recruit into the population as hatchlings at the beginning of the next annual cycle ( $N_{1,(t+1),fall}$ ). Also during summer, surviving population members ( $N_{1:5,t,sum}$ ) experience growth ( $\delta_{i,t}$ , cm TL). Based on sizes after growth, individuals transition ( $\psi_{1:4,t}$ ) to the next larger size class for the beginning of the next annual

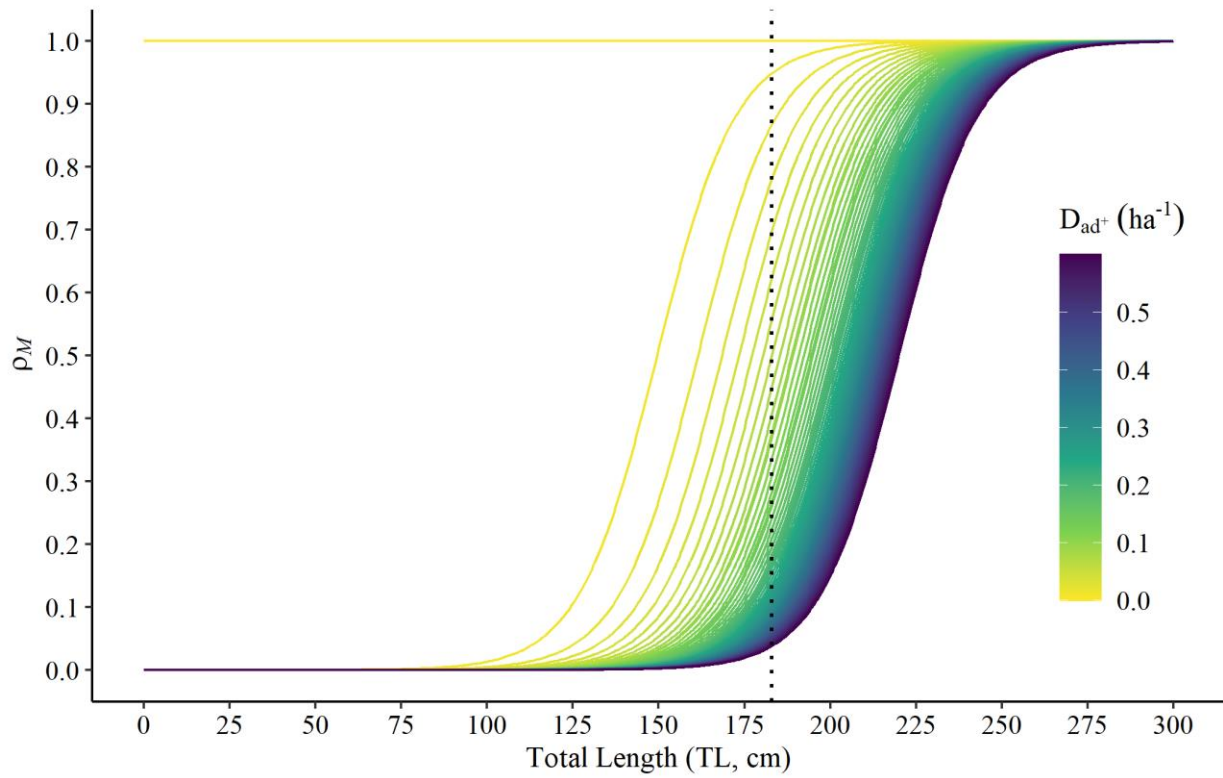
cycle,  $N_{z,(t+1),fall}$ . After summer, recently harvested alligators transition to the latent dead state 9 ( $N_{9,(t+1),fall}$ ) where they remain for the duration of the simulation.





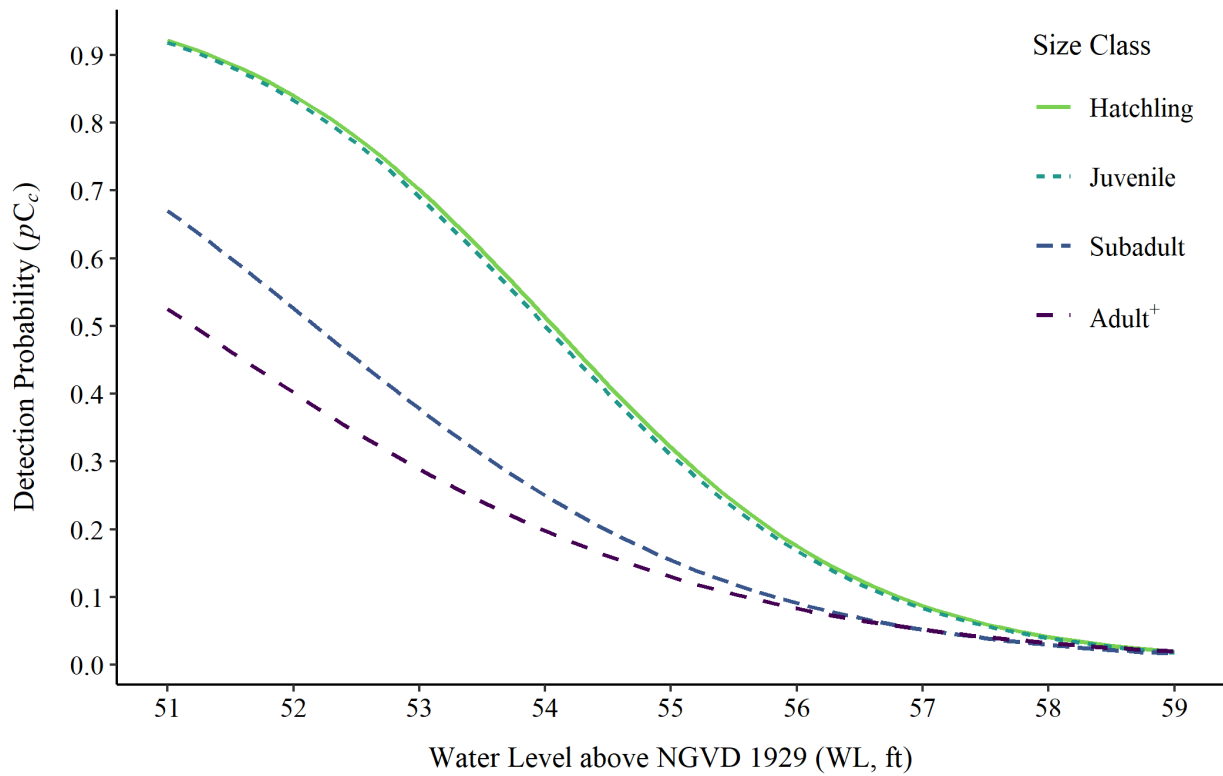
*Figure 3.4* Density-Dependent Survival Models

Density-dependent annual survival model by size class (color and line type) showing how annual survival after hunting season ( $\phi_c$ ) varies in relation to density of adult+ alligators. The gray vertical line marks the value used for intermediate density of adult+ alligators ( $D_0$ ) used as reference point for changes in density, 0.193, when deriving size-specific parameter values for the density-dependent survival models.



*Figure 3.5* Density-Dependent Puberty Model

Density-dependent puberty model describing the relationship between immature adult female size (total length, TL, cm) and the probability she reached sexual maturity in the past year ( $\rho_M$ ) as a function of the adult<sup>+</sup> population density ( $D_{ad+}$ ) in number per hectares. The vertical dotted line demarcates the subadult (< 122 cm TL) and adult ( $\geq$ 183 cm TL) size classes.



*Figure 3.6* Count Survey Detection Probability Models

Size class-specific relationships between water level (WL) and count survey detection probability on the logit scale:  $\text{logit}(pC_c) = \beta_{1,c} + \beta_{2,c}WL + \beta_{3,c}WL^2$  (Table 3.6). WL values span the range of WL observed at Orange Lake, FL, since 1981 (U.S. Geological Society, 2016).

$$\mathbf{tr} = \begin{bmatrix}
(1-\psi_H) \cdot \phi_{H,t} & \psi_H \cdot \phi_{J,t} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (1-\psi_H)(1-\phi_{H,t}) + \psi_H \cdot (1-\phi_{J,t}) \\
0 & (1-\psi_J) \cdot \phi_{J,t} & \psi_J \cdot (1-\lambda) \cdot \phi_{SA,t} & 0 & 0 & \psi_J \cdot \lambda & 0 & 0 & 0 & (1-\psi_J)(1-\phi_{J,t}) + \psi_J \cdot (1-\lambda)(1-\phi_{SA,t}) \\
0 & 0 & (1-\psi_{SA})(1-\lambda) \cdot \phi_{SA,t} & \psi_{SA} \cdot (1-\lambda) \cdot \phi_{A,t} & 0 & (1-\psi_{SA}) \cdot \lambda & \psi_{SA} \cdot \lambda & 0 & 0 & (1-\psi_{SA})(1-\lambda)(1-\phi_{SA,t}) + \psi_{SA} \cdot (1-\lambda)(1-\phi_{A,t}) \\
0 & 0 & 0 & (1-\psi_A)(1-\lambda) \cdot \phi_{A,t} & \psi_A \cdot (1-\lambda) \cdot \phi_{B,t} & 0 & (1-\psi_A) \cdot \lambda & \psi_A \cdot \lambda & 0 & (1-\psi_A)(1-\lambda)(1-\phi_{A,t}) + \psi_A \cdot (1-\lambda)(1-\phi_{B,t}) \\
0 & 0 & 0 & 0 & (1-\lambda) \cdot \phi_{B,t} & 0 & 0 & 0 & \lambda & (1-\lambda)(1-\phi_{B,t}) \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
H & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{bmatrix}$$

$$\mathbf{rho} = \begin{bmatrix}
p_H & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (1-p_H) \\
0 & p_J & 0 & 0 & 0 & 0 & 0 & 0 & 0 & (1-p_J) \\
0 & 0 & p_{SA} & 0 & 0 & 0 & 0 & 0 & 0 & (1-p_{SA}) \\
0 & 0 & 0 & p_A & 0 & 0 & 0 & 0 & 0 & (1-p_A) \\
0 & 0 & 0 & 0 & p_B & 0 & 0 & 0 & 0 & (1-p_B) \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{bmatrix}$$

Figure 3.7 Marginalized MRR Likelihood Transition and Observation Matrices

Annual state transition matrix for alligators ( $\mathbf{tr}$ ) from summer  $t$  to summer  $t + 1$ , and state-specific recapture and recovery probabilities for marked alligators ( $\mathbf{rho}$ ). In each matrix, rows correspond to latent state  $z = 1, 2, \dots, 9$ .

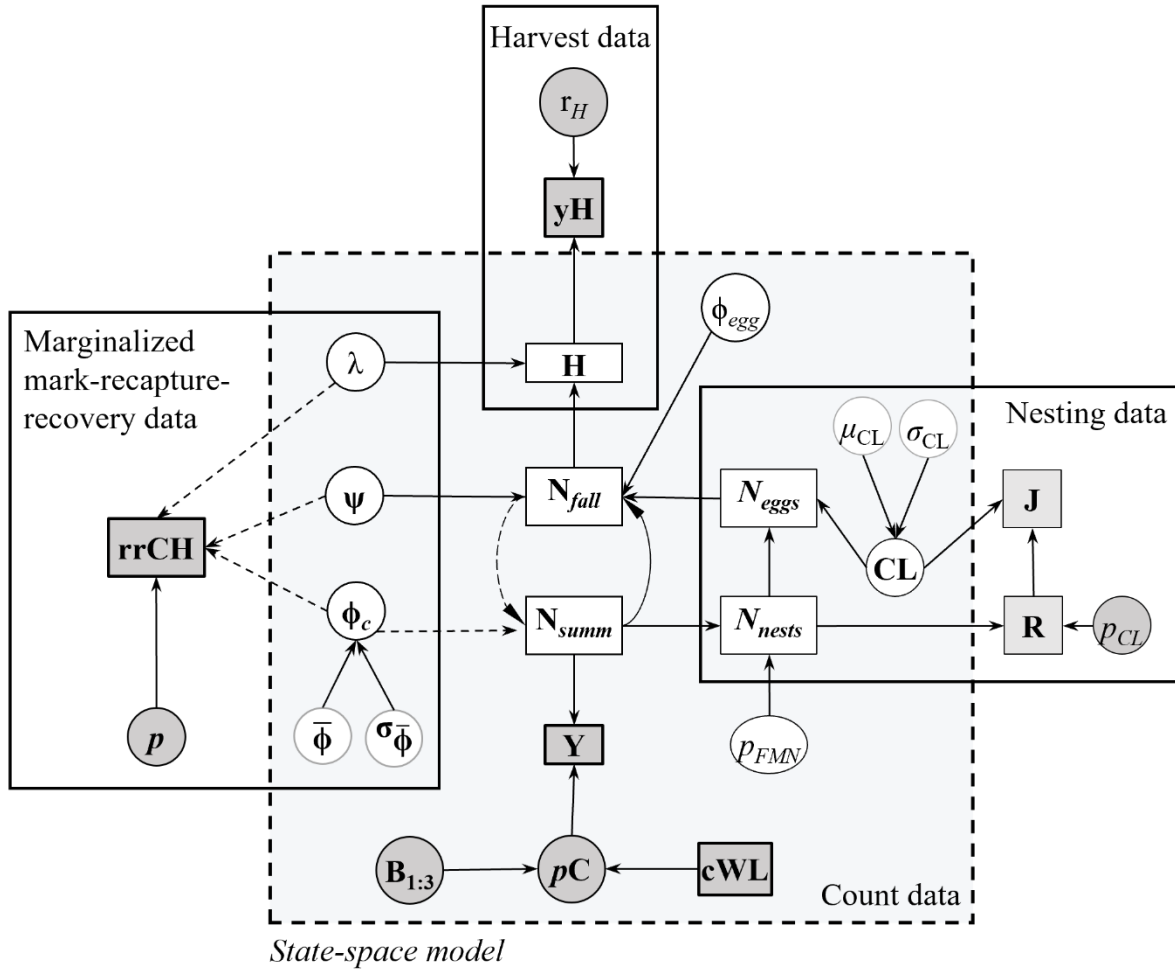
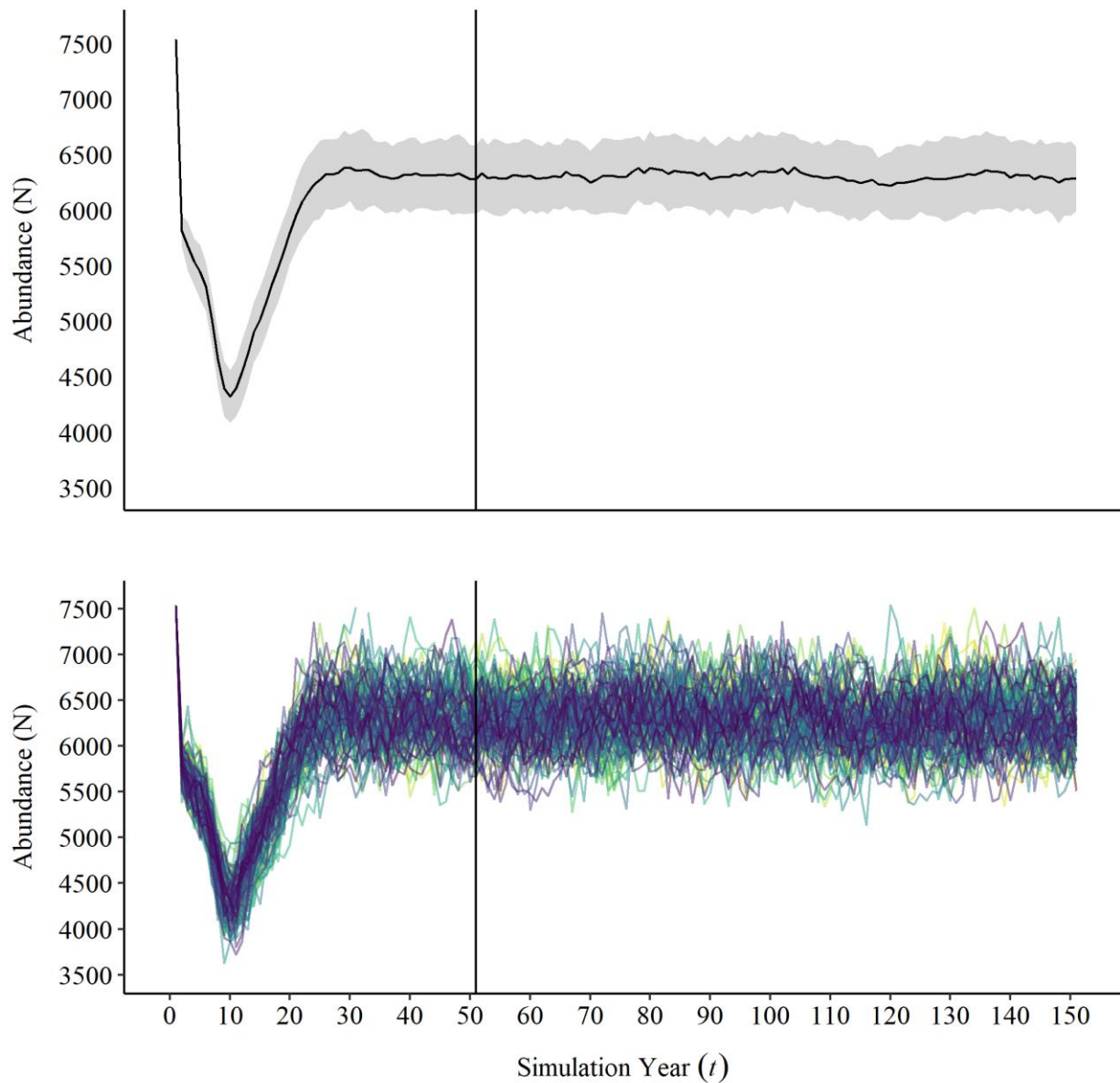


Figure 3.8 Estimation Model Directed Acyclic Graph

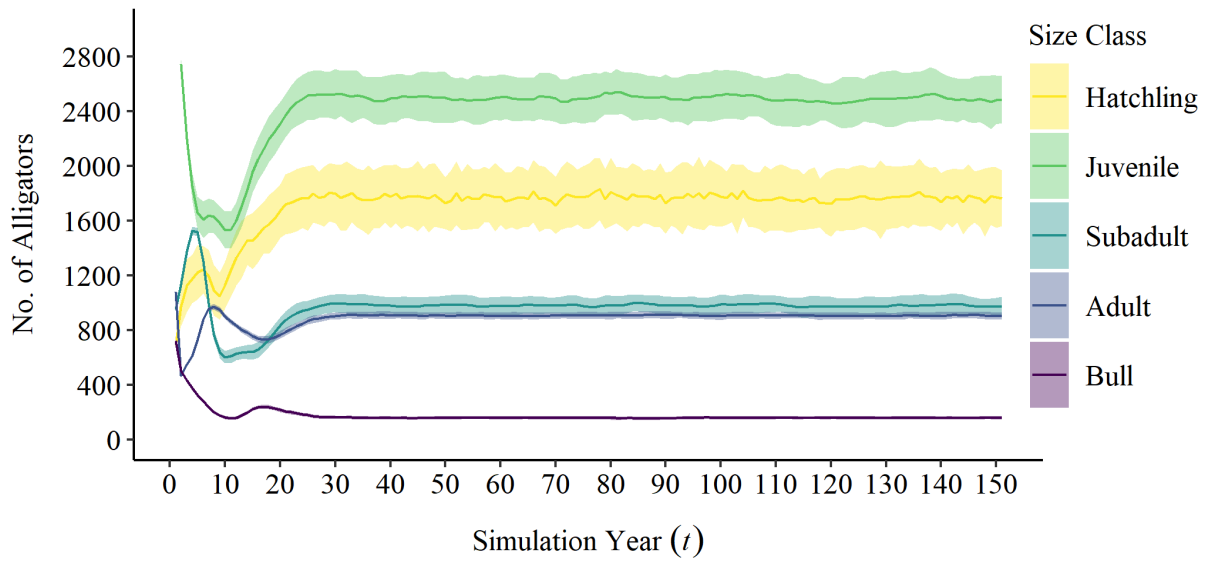
Relationships among the alligator IPM parameters (circles) in latent (white) and observation (gray) processes to which prior distributions were assigned and posterior distributions were monitored. Data are depicted in gray rectangles. White rectangles indicate latent population states. Matrices, vectors, and arrays are bold-faced and include matrices of size class-specific ( $c$ ) and annual ( $t$ ) values ( $\mathbf{N}_{fall}$ ,  $\mathbf{N}_{summ}$ ,  $\boldsymbol{\phi}$ ,  $\mathbf{yH}$ ), vectors of annual ( $t$ ) values ( $\mathbf{N}_{ad+summ}$ ,  $\mathbf{N}_{nests}$ ,  $\mathbf{N}_{eggs}$ ,  $\mathbf{R}$ ,  $\mathbf{J}$ ,  $\mathbf{CL}$ ,  $\mathbf{H}$ ), and vectors of size class-specific ( $c$ ) values ( $\bar{\phi}$ ,  $\sigma_{\bar{\phi}}$ ,  $\boldsymbol{\psi}$ ,  $\boldsymbol{p}$ ,  $\boldsymbol{\beta}_{1:3}$ ). The marginalized MRR data matrix,  $\mathbf{rrCH}$ , contains vectors associated with each unique capture segment ( $k$ ) from which the other MRR likelihood vectors (**first**, **last**, and **rrFR**; not depicted) are derived, along with the scalar value  $N_{MRR}$ . In the state-space model that describes the monitoring (count) data likelihood, arrays indexed by size class ( $c$ ), year ( $t$ ), and survey replicate ( $j$ ) include  $\mathbf{Y}$  and  $\boldsymbol{pC}$ , and the matrix  $\mathbf{cWL}$  contains values indexed by  $t$  and  $j$ . Scalar parameters include  $\lambda$ ,  $r_H$ ,  $p_{FMN}$ ,  $p_{CL}$ ,  $\mu_{CL}$ ,

$\sigma_{CL}$ ,  $\phi_{egg}$ . Refer to the Estimation Model section in the Chapter 3 Methods for a more complete description of the data likelihoods and parameter prior distributions, and see Table 3.10 for notation definitions.

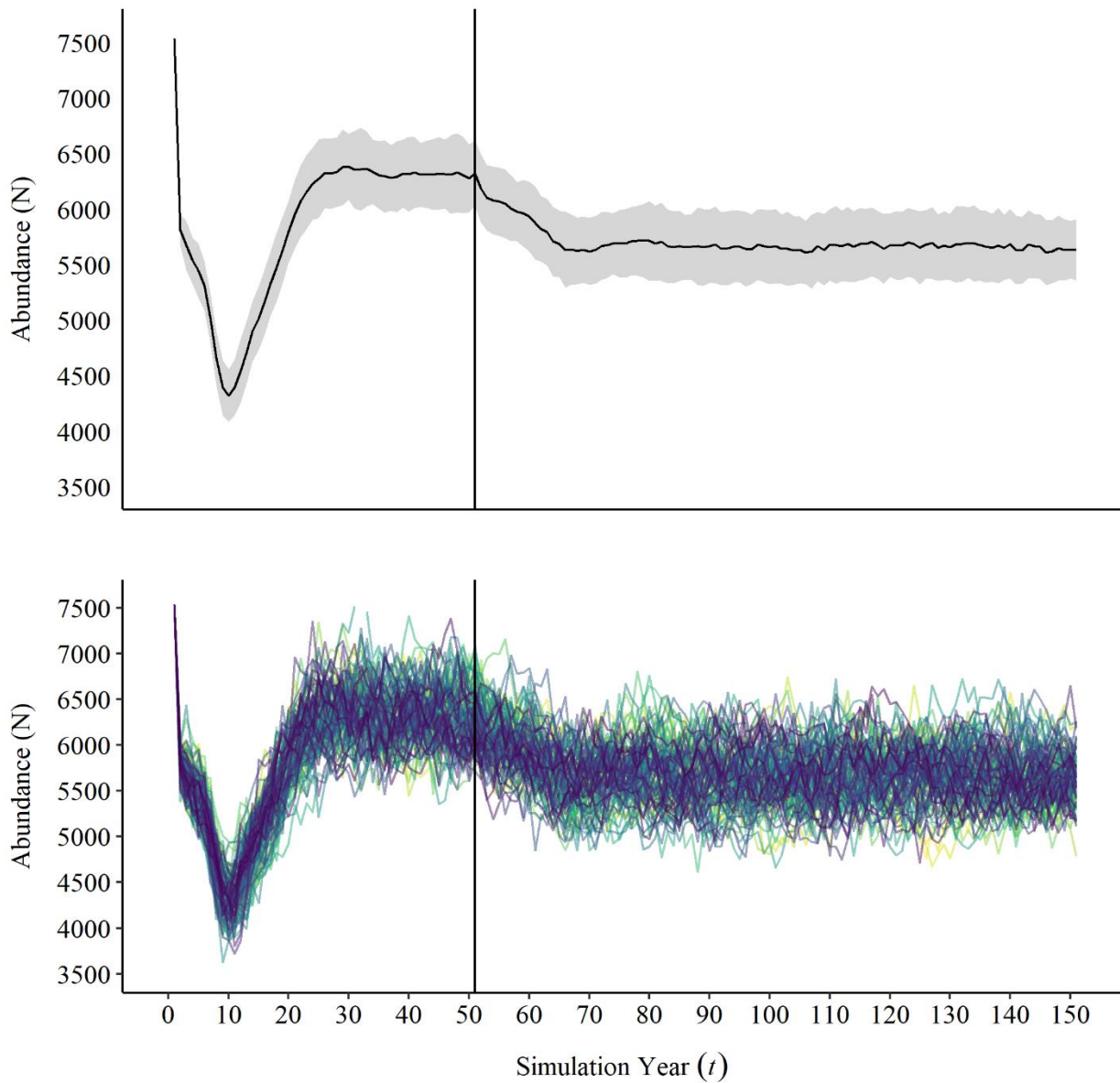


*Figure 3.9. Total Abundance Time Series Under a No-Harvest Policy*

Total number of individuals ( $N_t$ ) in the alligator population simulated over 150 annual timesteps. The top graph shows 100 stochastic replicate population time series. The top graph depicts the mean annual abundance (black line)  $\pm 1$  SD (shaded area) computed from 100 stochastic realizations of the population simulation model (bottom).

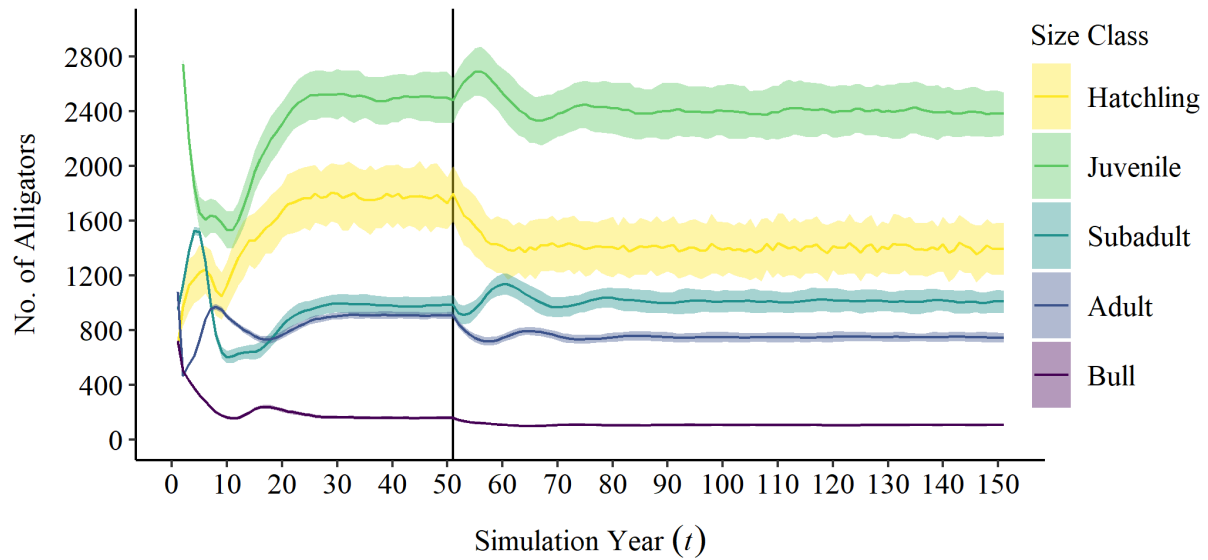


*Figure 3.10* Size Class-Specific Abundance Time Series Under a No-Harvest Policy  
 Summary of annual size class abundances in alligator population simulated without harvest. Solid colored lines mark the mean of 100 stochastic replicate simulations with lighter colored ribbons covering  $\pm 1$  SD from the mean.



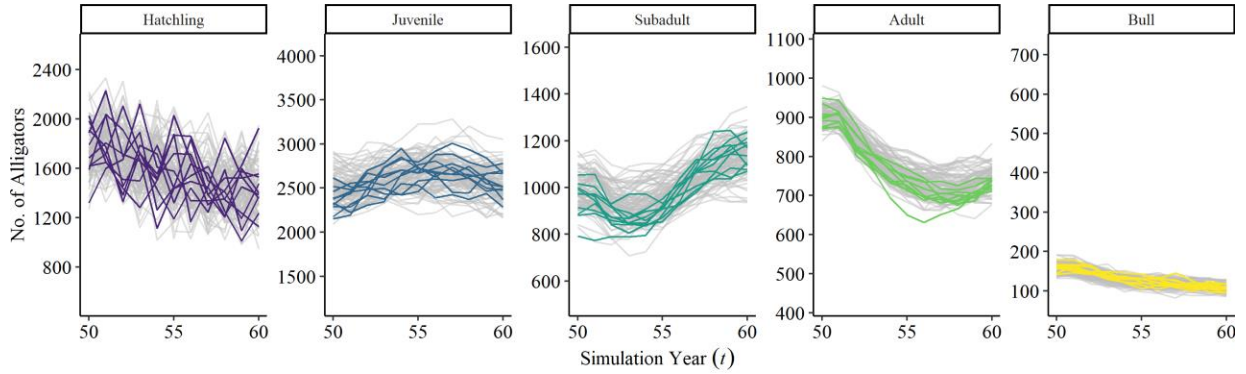
*Figure 3.11* Total Abundance Time Series for Population with a 13% Proportional Harvest Rate for Subadult<sup>+</sup> Alligators

Total number of alligators ( $N_t$ ) in the alligator population simulated over 150 annual timesteps. Mean annual abundance (top; black line)  $\pm 1$  SD (top; gray ribbon) for 100 stochastic population time series realizations (bottom) produced by the population simulation model with a constant annual proportional harvest of subadult<sup>+</sup> alligators initiated in  $t = 51$  (vertical black line).

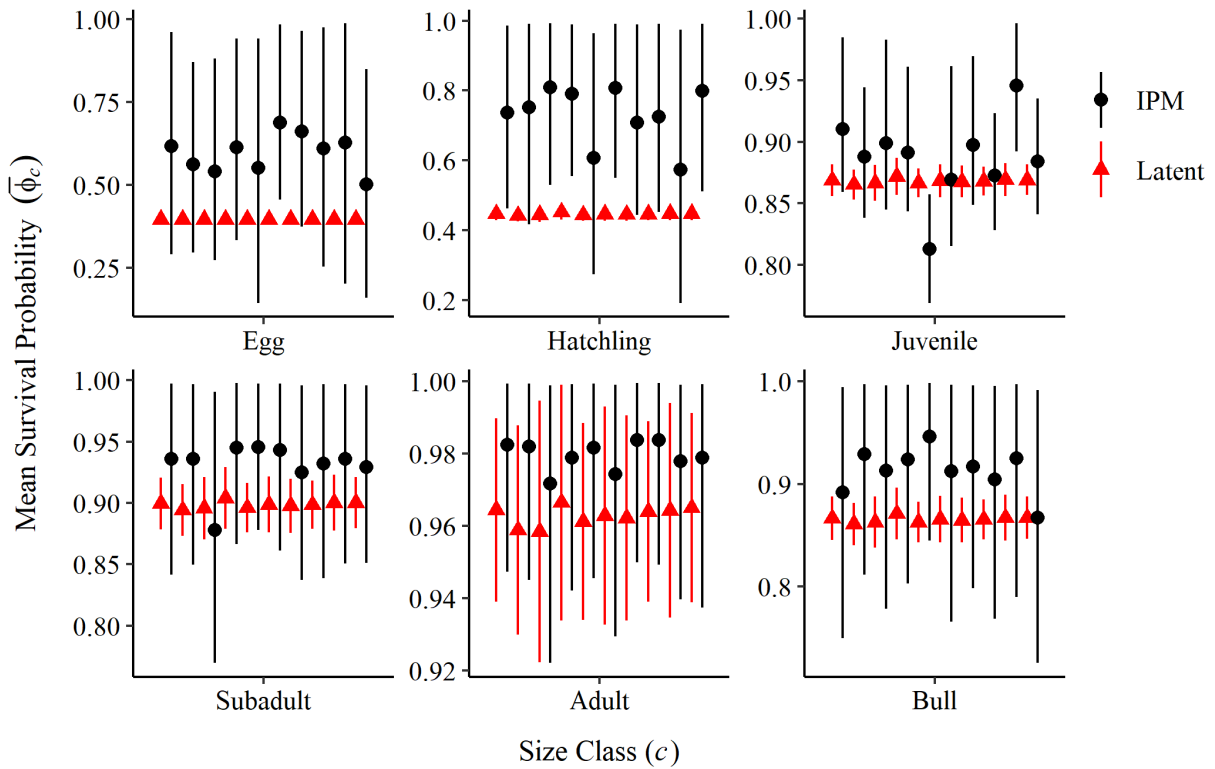


*Figure 3.12* Size Class-Specific Abundance Time Series for Population with a 13% Proportional Harvest Rate for Subadult<sup>+</sup> Alligators

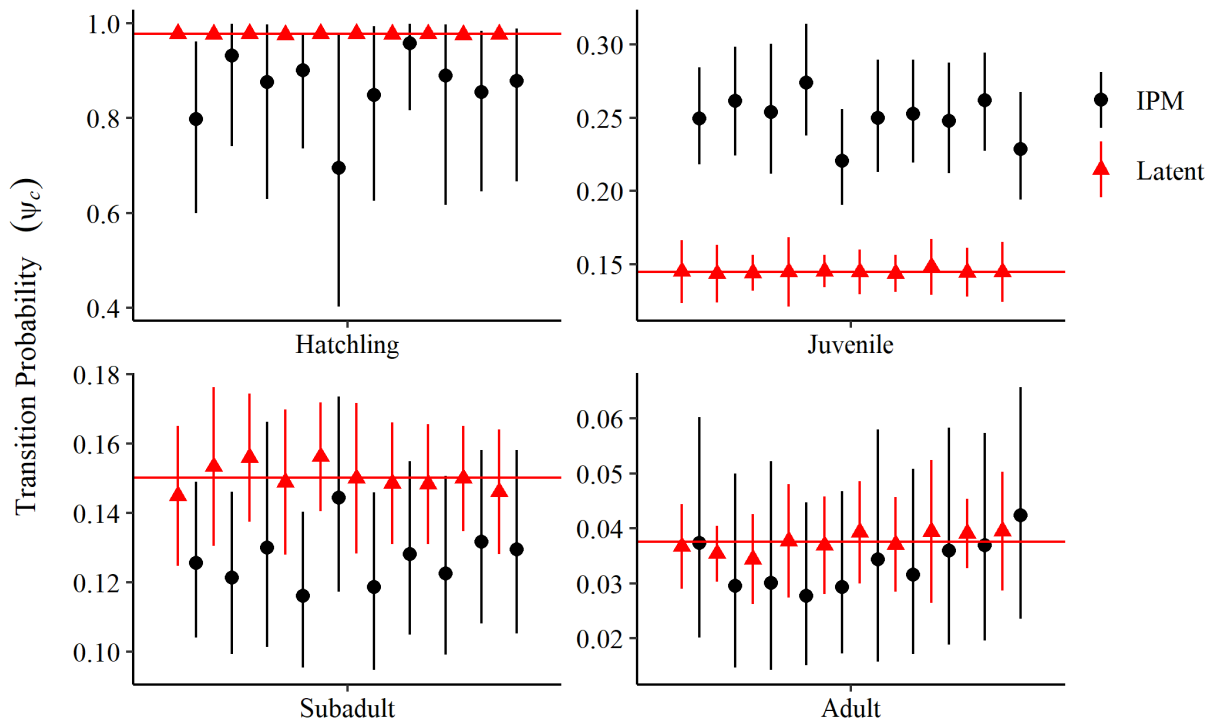
Summary of annual size class abundances in alligator population simulated over 150 annual timesteps with an annual proportional harvest of subadult<sup>+</sup> alligators initiated in  $t = t_{H0} = 51$  (vertical black line). Colored lines and the shaded ribbons depict mean annual size class abundance  $\pm 1$  SD of 100 stochastic replicate time series.



*Figure 3.13* Latent Size Class Abundance Time Series for Years Represented in IPM Data Sets  
 Size class-specific latent abundance time series produced by the population simulation model over the first ten years of harvest, which corresponds to the study period represented in the IPM trial data sets. One hundred stochastic replicates (gray lines) are shown with the time series from which the IPM trial data were simulated ( $n = 10$ ) highlighted (color lines).

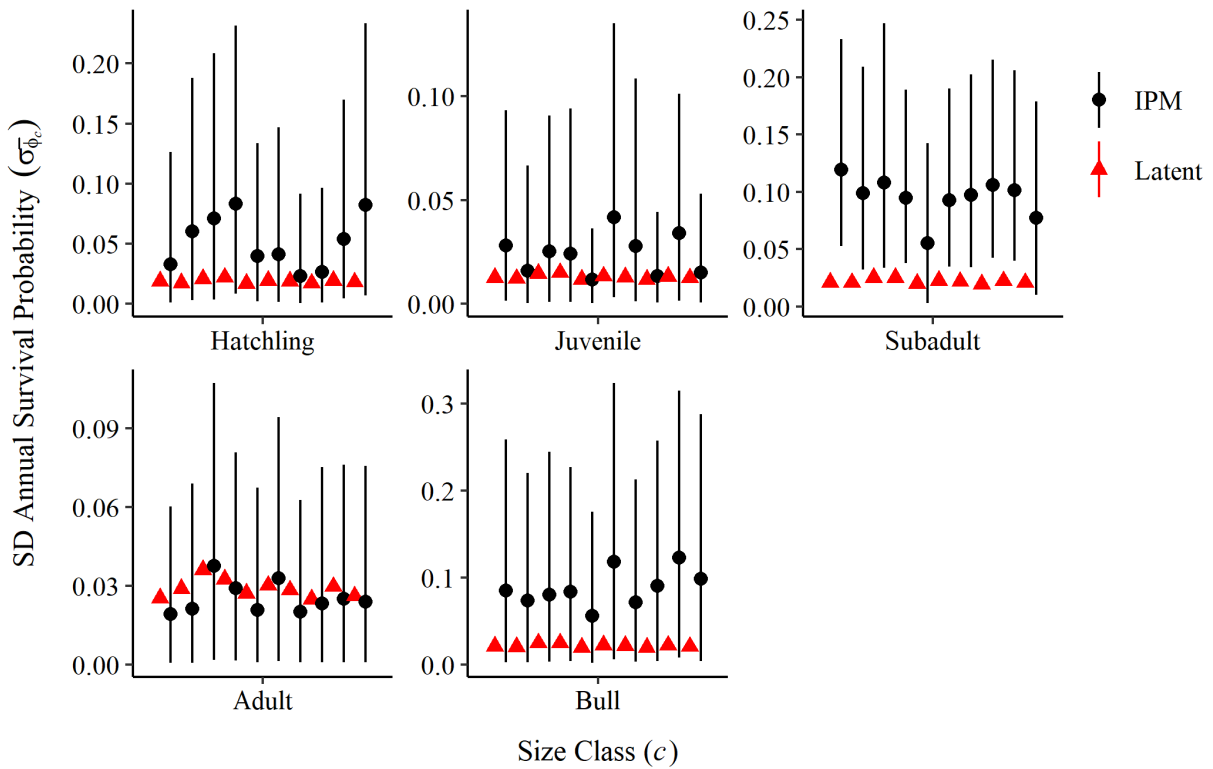


*Figure 3.14* Comparison Between IPM Posterior Estimates and Latent Survival Probabilities  
 Comparison between latent and estimated values for each size class ( $c = \text{Hatchling, Juvenile, Subadult, Adult, Bull}$ ) and eggs in nests (Egg). Average expected annual size class-specific survival rates ( $\bar{\phi}_c$ ) were computed from one hundred ( $n = 100$ ) realizations of the latent population (red triangle circles)  $\pm$  1SD (red error bars) for each of ten trials are presented along with trial-specific IPM posterior distribution mean (black circles) and 95% BCI (black error bars) for each trial. Values for  $\phi_{\text{egg}}$  were calculated from records of realized latent annual egg survival rates while latent values for  $\bar{\phi}_c$  were calculated for each trial by averaging the expected annual survival probabilities ( $\phi_{c,t}$ ) calculated each year over years spanned by replicate IPM data sets from the density-dependent survival model in the latent population simulation model. Note: different ranges plotted on y-axes for different size classes.



*Figure 3.15* Comparison Between IPM Posterior Estimates and Latent Size Class-Specific Transition Rates

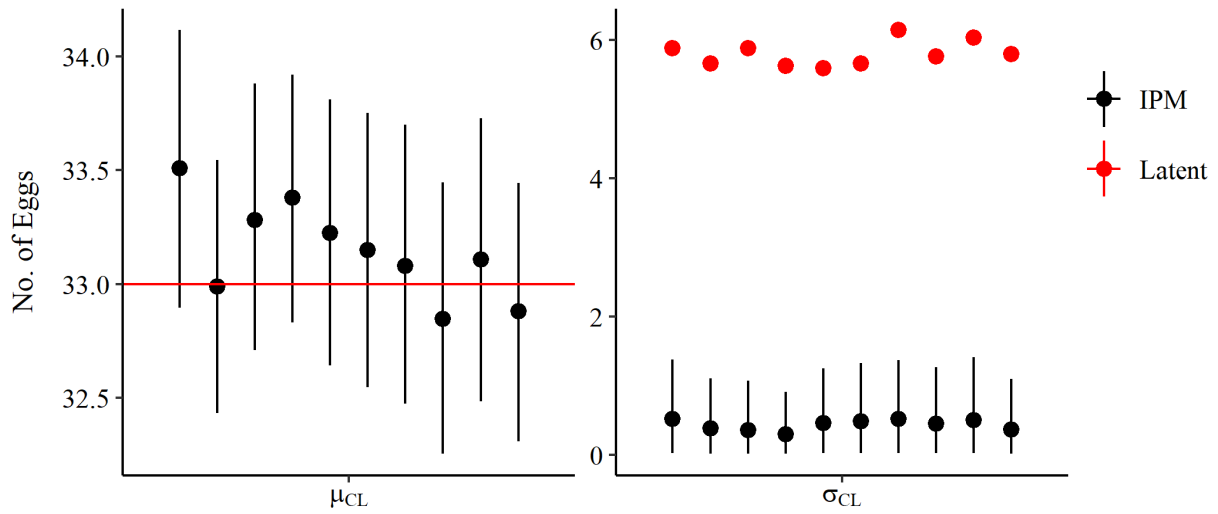
Comparison of mean (black circles) and 95% BCI (black error bars) of draws from the posterior distributions for size class-specific annual transition rates ( $\psi_c$ ) from ten trials and latent means (red triangles)  $\pm$  1 SD (red error bars) calculated for each trial based on latent records of realized transition rates averaged over years in the study period. The grand mean averaged over years ( $n = 10$ ) and trials ( $n = 10$ ) for each size class is marked with a horizontal red line.



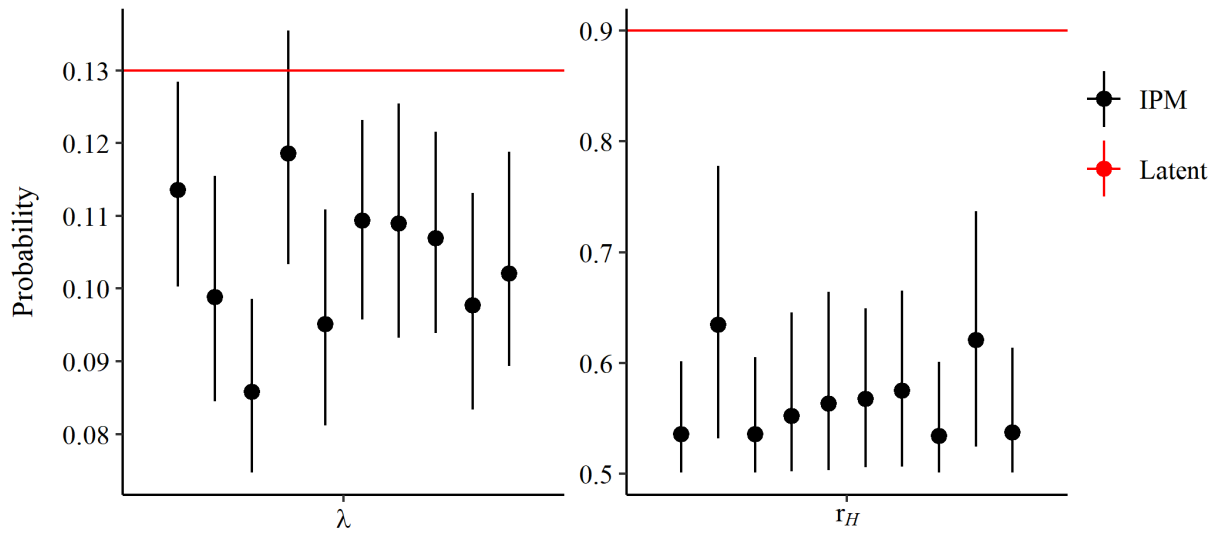
*Figure 3.16* Comparison Between IPM Posterior Estimates and Latent SD of Size Class-Specific Survival Probabilities

Comparison between latent and estimated values for the standard deviation (SD) around mean survival rate ( $\bar{\phi}_c$ ) for each size class ( $c = \text{Hatchling, Juvenile, Subadult, Adult, Bull}$ ). Latent values (red triangles) for each of ten trials are presented relative to the mean (black circles) and 95% BCI (black error bars) of draws from the posterior distribution for ( $\sigma_{\bar{\phi}_c}$ ) for each trial.

Latent values derive from trial-specific SDs calculated from expected annual survival probabilities ( $\phi_{c,t}$ ) produced by the density-dependent survival model for each size class in the population simulation model over the years spanned by replicate IPM data sets.

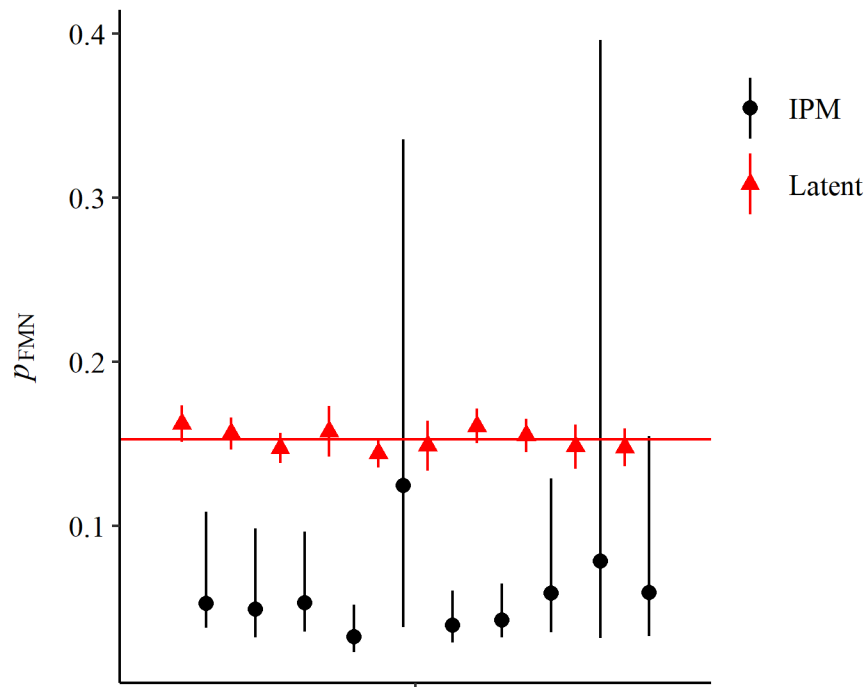


*Figure 3.17* Comparison Between IPM Posterior Estimates and Latent Mean Clutch Size  
 Comparison of mean and 95% BCI (= black circles and error bars) of draws from the posterior distributions for expected clutch size ( $\mu_{CL}$ ; left) and the SD of expected clutch size ( $\sigma_{CL}$ ; right) from IPM trials ( $n = 10$ ) relative to the latent value for CL (33) specified *a priori* in the latent population simulation model (horizontal red line; left) and the latent realized mean clutch size  $\pm$  1 SD (red circles; right). Note: The SD error bars associated with latent  $\sigma_{CL}$  are small enough that they are encompassed by the mean circles.



*Figure 3.18* Comparison Between IPM Posterior Estimates and Values for Annual Harvest Probability and Hunter Harvest Reporting Rate

IPM posterior distribution means (black circles) and 95% BCIs (error bars) for annual harvest probability for subadult<sup>+</sup> alligators during hunting season ( $\lambda$ ) and hunter harvest reporting rate ( $r_H$ ) from ten trials relative to latent parameter values specified *a priori* in the latent population simulation model ( $\lambda = 0.13$ ) and harvest data simulation model ( $r_H = 0.90$ ) (horizontal red lines).



*Figure 3.19* Comparison Between IPM Posterior Estimates and Latent Proportion of Nesting Females

Comparison of means and 95% BCI (black circles and error bars) of draws from the posterior distributions for the proportion of the adult<sup>+</sup> population made up of mature nesting females ( $p_{FMN}$ ) from ten trials and latent means  $\pm 1$  SD (solid triangles and error bars) of realized nesting proportion of adult<sup>+</sup> size classes over years in the study period ( $n = 10$ ). The grand latent mean averaged over years ( $n = 10$ ) and trials ( $n = 10$ ) is marked with a horizontal red line.

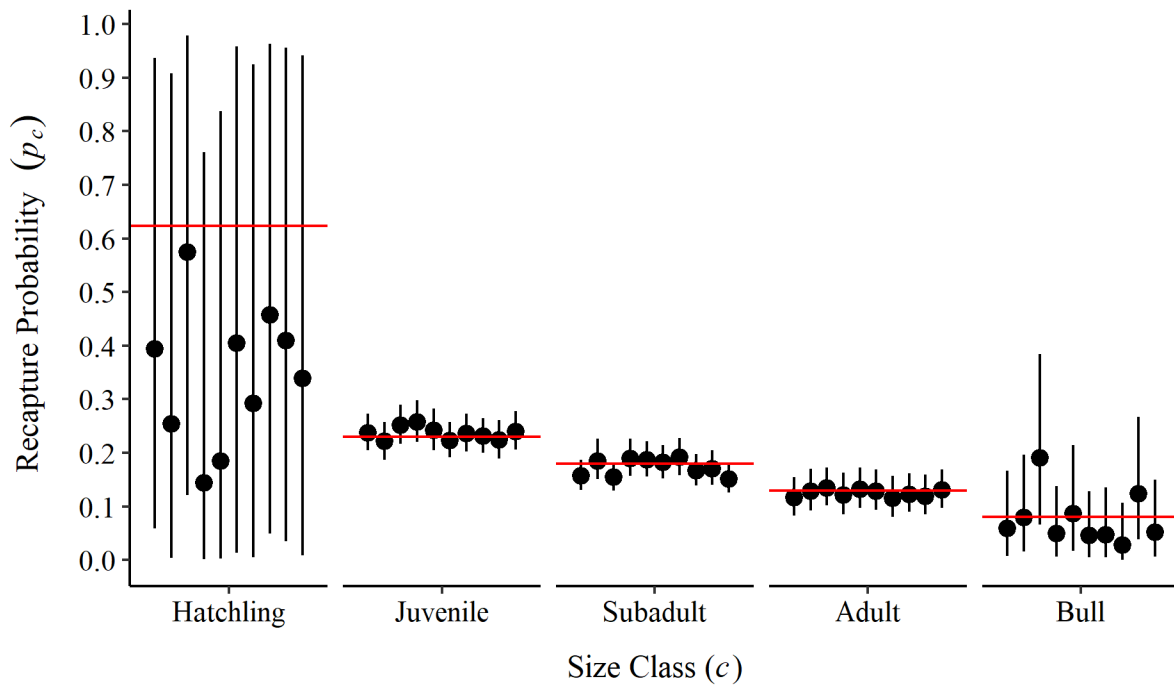
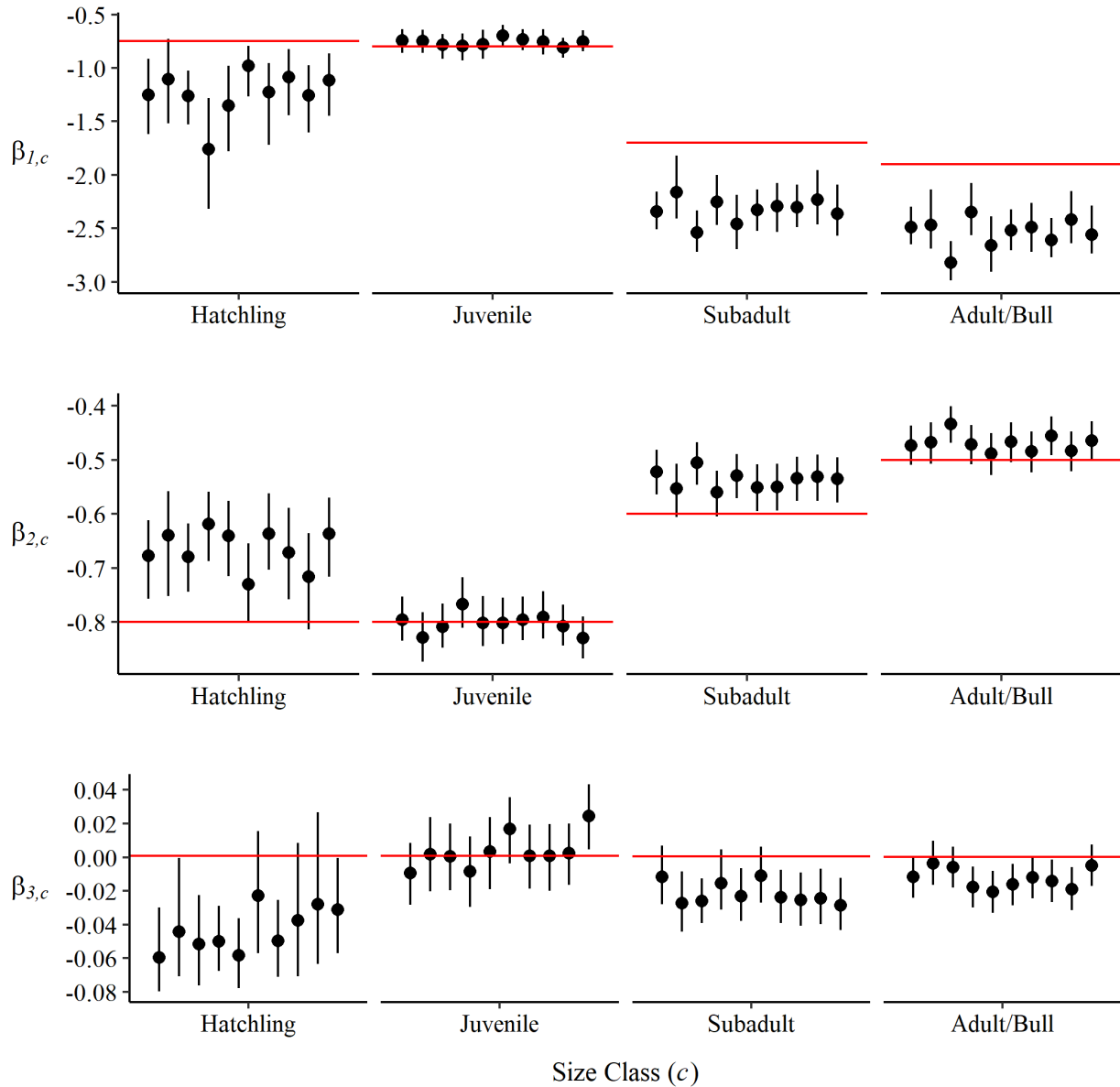


Figure 3.20 Comparison Between IPM Posterior Estimates and Latent Recapture Probabilities Mean (black open circles) and 95% BCI (error bars) of draws from the posterior distribution for size-specific recapture rates for marked individuals ( $p_c$ ) from ten IPM trials compared to latent values for  $p_c$  specified *a priori* in the MRR data simulation model (horizontal red line).



*Figure 3.21* Comparison Between IPM Posterior Estimates and Latent Values for Detection Probability Model Coefficients on Logit Scale

Mean and 95% BCI (black circles and error bars) of the posterior distribution estimates for the size class-specific count survey detection probability model coefficients, on the logit scale ( $\beta_{1:3,c}$ ), from IPM trial data sets ( $n = 10$ ) relative to latent parameter values specified *a priori* in the data simulation model (horizontal red lines; Table 3.6).

## CHAPTER 4

### **Optimizing Recreational Alligator Harvest Quotas with Approximate Dynamic Programming**

The American alligator (*Alligator mississippiensis*) occupies a distinct niche in native ecosystems and the public psyche. As an ecosystem engineer and apex predator, the alligator plays critical ecological roles in freshwater and wetland systems across the southeastern US. The species also provides consumptive and non-consumptive recreational opportunities, hunting and wildlife viewing, respectively. For alligator managers, management policies are pursuant to multiple objectives, and priorities vary regionally.

Generally, for predator populations, wildlife agencies seek an upper limit to abundance that moderates public complaints and fear, and a lower limit that preserves the species in perpetuity (Tyre & Michaels, 2011). For alligators specifically, the upper limit incorporates a harvestable surplus that sustains recreational hunting opportunities without compromising other benefits and services. Identifying policies with potential to achieve a satisfactory balance across management objectives requires knowing the current value of the resource and its potential for improvement through management actions or policies. This means understanding how the management system functions and generates positive or negative outcomes for stakeholders (Decker et al., 2012).

For many species, insufficient population data inhibits science-based decision making. For others, such as the American alligator, which has been the focus of research and monitoring efforts for multiple decades, science-based decision guidance is hindered by complex species

ecology and limitations inherent to agencies' current decision-making practices. For well-defined problems, quantitative methods can identify optimal decision alternatives pursuant to multiple objectives involving tradeoffs, such as those that emerge between near- and long-term aspirations, and extractive and non-extractive activities.

My aim in this chapter was to identify a harvest policy function to optimize annual harvest quotas for alligators in service of management objectives based on a biological modeling framework with direct links to existing monitoring protocols. Pursuant to the question of what policy function is optimal for identifying annual alligator harvest quotas based on observed population state, biological mechanisms of population change, and long-term harvest management goals, my objectives were as follows:

1. Develop an alligator population model consistent with scientific understanding of species population biology and responses to harvest;
2. Specify an objective function describing preferred management outcomes; and
3. Identify parameter values for a harvest policy function that uses annual count data to set annual harvest quotas, which optimize the objective function despite uncertainty about true system state (population abundance) and future population trajectory.

In the following section, Background, I provide more context for the analysis presented in this chapter. First, I describe common features of recreational alligator harvest programs managed by different agencies in the species eastern range. Then, I explain how agencies currently set quota limits and issues with existing approaches. From there, I present my methodology with a succinct description of the theory and tools underlying my approach to developing a science-based harvest policy for optimizing annual alligator hunting regulations.

## Background

### *Alligator Harvest Management*

In the eastern portion of the alligator's range, specifically Alabama, Florida, Georgia, and South Carolina, a significant portion of annual harvest occurs on public land and agencies share a resource management legacy. Recreational alligator harvest programs vary in size and structure by state due to differences in agencies' ecological, social, and institutional contexts, and program histories. The hunting season in all four states begins towards the end of the growing season after most alligator nests have hatched, in mid-August or early September. Exact season timing, duration, daily hunt hours, and allowable methods of lethal take (i.e., dispatch of individual animals) vary.

Harvest management decisions for alligators primarily involve setting limits (quotas) on total allowable take each hunting season (i.e., how many alligators of harvestable size can be removed from the population by hunters). In most states, take is restricted to non-hatchlings, or subadult, adult, and bull size classes (subadult<sup>+</sup>;  $\geq 122$  cm total length, TL). In Florida, the Florida Fish and Wildlife Conservation Commission (FFWCC) also allows limited take of wild eggs and hatchlings, primarily to stock ranching operations that supply commercial meat and hide markets, but the agency regulates egg and hatchling collection independently from public harvests of larger size classes.

Agencies distribute the total annual allowable take among harvest units through unit-specific hunt quotas. The FFWCC sets harvest quotas for numerous small alligator management units (AMUs), i.e., at the scale of individual waterbodies (tens of km<sup>2</sup>). Other agencies in the species eastern range manage harvest across multi-county units that extend over large geographic areas (thousands of km<sup>2</sup>) and are typically delineated along watershed boundaries. In South

Carolina the statewide quota is evenly distributed among harvest units, but agencies in Alabama, Florida, and Georgia set harvest unit quotas according to each agency's understanding of the proportion of the state's alligator population contained therein as best they can determine based on population counts, trends, and area-specific harvest results.

When establishing their respective harvest programs for alligators, agencies arrived at initial quotas through different means. Some analyzed long-term count data and set quotas as a percentage of abundance estimates while others based initial quotas on their intuition then monitored annual counts for signs that quotas were unsustainable. The FFWCC conducted an experimental harvest (1981 – 1990) (Woodward et al., 1992).

Across programs, quota levels and harvest rates are relatively stable year-to-year despite consistent discrepancies between quota limits and harvest totals, reflecting managers' partial control of the system. Quotas regularly go unfilled. Managers attribute low hunter success rates, defined as the number of hunter-harvested alligators divided by the quota as a percentage, to a combination of factors. Sometimes applicants selected for an alligator tag do not pay their permit or license fee(s). In other cases, trophy hunters pass opportunities to take an animal at the smaller end of the permitted size range limit, then fail to take a larger animal during the limited-duration hunting season.

Recognizing the discrepancy between the quota and number of alligators taken by hunters each hunting season, some agencies set more liberal quotas to allow for more permits to be available for the public. Other agencies maintain quota levels barring a remarkable deviation in annual population counts. Overreliance on habit or tweaking the status quo requires modest effort and minimal risk, but it is one of the most common pitfalls in organizational decision-making (Gregory & Keeney, 2002).

### *Quota Selection*

As far back as the late 1980s, when the FFWCC, formerly the Florida Game and Fresh Water Fish Commission, initiated its statewide recreational alligator harvest program, managers recognized issues with using quota harvests to manage alligator populations (Woodward et al., 1992). Regardless of whether partial controllability is formally considered, setting quotas to reach a particular population target requires a mechanistic population model describing demographic processes (Woodward et al., 1992). As mentioned previously, population models help forecast management outcomes (i.e., consequences) under different decision scenarios (e.g., quota limits), which provides managers with valuable insights about population responses and the nature and magnitude of tradeoffs associated with different levels of harvest. Past attempts to model alligator population dynamics, described in more detail in the Background section of Chapter 3, fell short of producing reliable population harvest models capable of forecasting population responses to alternative management strategies (Nichols, Chabreck, et al., 1976; Nichols, et al., 1976; Taylor & Neal, 1984; Woodward, 1996b).

Lacking models capable of predicting management outcomes, decisions regarding annual harvest-unit quota levels are based predominantly on statistical trends in population index values, i.e., counts of individuals with no statistical adjustment for present but missed individuals, derived from night spotlight counts of alligators. Managers rely on their judgement of trends in monitoring and hunter harvest data, often without accounting for sources of uncertainty inherent to management system dynamics and the partial observations of those dynamics captured in population data. Management agencies acknowledge the inadequacy of setting harvest policies based on trends in population index values, although the FFWCC uses covariate data to account for variation in detection due to varying survey conditions. Annual hunter success rates and

nuisance alligator reports influence quota decisions at some agencies, albeit indirectly because a mechanism to formally integrate these data streams with population index values is absent in current decision processes.

The FFWCC and the Georgia Department of Natural Resources (GADNR) adjust harvest quotas according to criteria set out in their respective management program proposal and plan, respectively. In both cases, *a priori* decision thresholds relate agency monitoring data to changes in the available quota within each harvest unit. The FFWCC relies on “action zones,” harvest unit-specific population abundance thresholds defined relative to a pre-harvest (1988) population size estimate for each unit. The thresholds serve as decision triggers to adjust the quota up or down by set percentages depending on where the most recent population size index from count survey data, adjusted for imperfect detection using a unit-specific estimation model, falls relative to the thresholds. The GADNR adjusts harvest unit quota levels based on the relative positions of the most recent population index value from count surveys and pre-defined “closure”, “restriction”, and “liberalization” points that they established for each harvest unit using the unit-specific index value averaged over the decade (1999 – 2009) preceding development of the Georgia Alligator Management Plan (2010). The programs in Alabama and South Carolina rely on expert judgment to translate relative abundance indices and trends into an adjustment of the quota.

Agencies share a desire to safeguard against arbitrary and capricious decisions, and to minimize the likelihood of unexpected and undesirable outcomes in the future. Their current approaches are problematic for several reasons: they are retrospective, ignore species biology, and do not account for sources of uncertainty inherent to scientific inferences from population and management data and their use in decision making. Consequently, existing practices do little

to reduce uncertainty regarding how managers should respond to unexpected departures from monitoring data trends.

Trend analyses are insufficient for decision making because they offer a retrospective vantage point with no means to interpret the observed system state (i.e., population count) as a “leading indicator” of a population surge or crash. Population counts from spatially restricted survey routes are assumed representative of population abundance within or across harvest units, but quota deliberations rarely, if ever, account for uncertainty regarding the veracity of this assumption. Population indices have recognized limitations, one of which is that they do not account for discrepancies that may exist between the inferences made from survey data and population dynamics at larger spatial scales targeted by management. Further, count data trend models are poor predictors of likely future population states because they do not account for the biological mechanisms of population change, e.g., survival, growth, and reproduction. Rather, they describe a phenomenological relationship between observations without a clear understanding of how observations relate to true latent population states, and that relationship may vary based on unrecognized factors. Observing a jump or dip in count survey data relative to a historic trend is only informative if survey data reliably represent the population targeted by management actions. Otherwise, it contributes to management uncertainty because the jump or dip cannot be explained in terms of population mechanisms. A trend-based approach may also be inadequate for alligators given the species’ stage-class structure, which likely causes time lags between management actions and population responses.

Current approaches also overlook the possibility of unanticipated management outcomes resulting from uncertainty arising from imperfect knowledge of the resource and the management system. Without a formal means to account for different sources of uncertainty,

managers cannot quantify the risk associated with different courses of action. Lacking analytical tools, managers acknowledge the effects of environmental and demographic stochasticity, and make decisions based on their risk tolerance, potentially choosing options that are believed to be safe under a range of scenarios. Agencies in our study often default to primarily adopt a precautionary approach to alligator harvest management that implicitly prioritizes a long-term resource sustainability objective. In so doing, tradeoffs are made with other management objectives in unacknowledged ways, and actions chosen today may eliminate future possible actions, so-called opportunity costs.

To anticipate management consequences, managers need a mechanistic population model inclusive of the demographic processes responsible for population dynamics. An approach that is closely tied to clearly articulated objectives and that explicitly considers monitoring data in a biological context may allow agencies to maximize public benefits and minimize the likelihood of undesirable surprises. The goal for managers then is to develop a decision rule, or policy function, capable of identifying an optimal policy or action for each possible system state at each decision point based on articulated objective(s) (Williams & Johnson, 2013). From one hunting season to the next, the policy recommendation varies depending on the timing and/or the state of the system.

### ***Markov Decision Processes and Optimization***

Recurrent resource management decisions, such as setting annual hunting limits, are described as Markov decision processes (MDPs). Markovian systems are stochastic and serially correlated; the system at any point in time is a function of the system at the preceding time point and variability inherent to system dynamics, i.e., stochasticity. In renewable resource management systems, MDPs are influenced by (a) our ability to measure the system, and (b) our

understanding of system dynamics. The biological system is only partially observable. Monitoring data generate uncertainty about population size or status (system state) due to imperfect detection in annual population counts. Incomplete understanding of how population size relates to demographic processes and environmental factors underlie structural uncertainties that affect how the system dynamics are modeled.

To aid sequential decision making under uncertainty, dynamic optimization combines a model of system change with objective functions that assign value to present and future consequences of alternative decision options (Williams & Johnson, 2013). Dynamic programming (DP), a form of dynamic optimization, identifies an optimal policy by dividing complex MDPs into subproblems and determining which policy produces an optimal solution for all subproblems (Mes & Rivera, 2017, pp. 63–101). The capacity to explore variability generated in and among subproblems makes dynamic programming well-suited for systems with stochastic behavior. Able to generate feedback policies, DP can identify optimal decisions for not only expected future states but possible future states (Williams & Johnson, 2013).

Because dynamic programming requires discrete representation of all modelled components, DP falls apart in systems with complex state structures, such as alligator populations. Alligator ecology and physiology change over the course of an individual's life, based on its size. As a slow-growing, long-lived species, alligators remain in life stages, typically delineated by individual total length (TL, cm), for multiple years at a time. The five commonly used life stages (states, or size classes). include: hatchlings, juveniles, subadults that are subject to harvest but not sexually mature, adults that are both harvestable and capable of reproducing, and very large primarily male bulls (see Table 3.1 for TL size class ranges).

The “curse of dimensionality” often makes computing an exact solution to an MDP difficult or impossible (Mes & Rivera, 2017, pp. 63–101). As the number of population states increases, the state space grows exponentially in the number of state variables necessary to encompass possible paths to alternative future states, which proportionally increases computational requirements (Ohno et al., 2016). A standard work-around for the issue of dimensionality for discrete state spaces has been to simplify the system model to its essential elements, but even the simplest representation of complex systems such as alligator populations may overwhelm dynamic programming computational platforms. This suggests a need for an alternative approach for solving large-scale multistate stochastic MDPs. A simple stochastic modeling approach using forward simulation, such as approximate dynamic programming (ADP), may be a viable option.

In this chapter, I use Approximate Dynamic Programming (ADP) to identify an optimal harvest policy for setting annual alligator harvest quotas. ADP approximates the optimal solution of MDPs using a diverse portfolio of computational methods that distinguish themselves from one another in terms of the type of value function approximation and policies involved (Mes & Rivera, 2017, pp. 63–101). For complex, recurrent, stochastic optimization problems, ADP provides a robust modeling framework for issues arising from the “curse of dimensionality.”

I rely on a genetic algorithm optimizer that imitates the primary processes responsible for the evolution of living organisms: natural selection and sexual reproduction (Holland, 1992). Genetic algorithms (GA), initially developed in the 1960’s, provide a stochastic, evolutionary computation method for solving complex optimization problems (Holland, 1992). In an optimization programming context, evolution of a population of candidate solutions to the

optimal control problem occurs by way of simulated genetic operators (mutation and crossover) and population dynamical processes (e.g., reproduction and selection).

## **Methods**

### ***Harvest Management System***

This analysis was conducted using a simulated alligator management system with four key components: first, a system state model that describes the annual population processes responsible for population change over time; second, an observation model that generates annual monitoring data; third, a harvest policy decision that sets the annual hunt quota based on observed population state; and fourth, a harvest mortality process (Figure 4.1). For the first component, the system state model, I used the alligator population simulation model from Chapter 3. Briefly, the model simulates a population representing the alligator population at Orange Lake (OL) in north-central Florida. OL was one of three treatment lakes in the FFWCC's experimental harvest of commercial-size alligators ( $\geq 122$  cm total length, TL) conducted between 1981-1990.

The population model simulates the demographic processes responsible for alligator state transitions over time, including survival, reproduction, and growth (see Chapter 3 Methods). A management model constituted by the second, third, and fourth components of the system interacts with the population simulation model in each annual time step. Each component of the management model is described next, followed by a description of the optimization procedure. For details about the population simulation model see Chapter 3. Notation defined in the following methods sections are listed with their description in Table 4.1.

## **Management Model.**

**Population Monitoring.** The first step in the management model is an observation process that generates information about current population state, defined here as the number of harvestable alligators in the population before harvest in year  $t$  ( $Nh_t$ ), in the form of monitoring data. Due to imperfect detection,  $Nh_t$  is only partially observable, so management decisions are based on the number of harvestable alligators observed during annual count surveys ( $yNh_t$ ), which are simulated from a binomial model with detection probability equal to 0.35.

$$yNh_t \sim \text{Binomial}(Nh_t, 0.35)$$

The value 0.35 is an arbitrary but reasonable value supported by monitoring studies (Woodward et al., 1992).

**Policy Decision.** Next, a harvest policy function uses annual count data ( $yNh_t$ ) to indicate the quota for the upcoming hunting season  $t$  ( $Q_t$ ). I proposed a logistic model for the policy function relating observed population state to a quota decision, so quotas shift in relation to changes in  $yNh_t$ . When the population is perceived to be low, the quota is low. When population levels increase, quota levels rise. As a logistic curve, the harvest policy function is described by three parameters, all constant with respect to time:  $\alpha$ , the slope at the inflection point, and  $\beta$ , the inflection point; and  $Q_{max}$ , the maximum total allowable take. Accordingly, the annual quota ( $Q_t$ ) was set with the following harvest policy function:

$$Q_t = Q_{max} / (1 + \exp^{-\alpha(yNh_t - \beta)})$$

**Harvest Implementation.** The final step in the management model implements harvest. Managers only have partial control over implementation of harvest quotas, which leads to discrepancies between intended management ( $Q_t$ ) and actual management outcomes (e.g.,  $H_t$ , total annual harvest). The number of hunter-harvested alligators in a season as a percentage of

the quota, or hunter success rate, at OL during the experimental harvest, averaged over all years of the study, 1981 – 1990, was 87.5%. I simulated the effects of partial controllability in the harvest implementation component of the management model using a binomial process with probability of hunter success equal to 0.875, which allowed me to translate the quota into realized hunter harvest for year  $t$  ( $H_t$ ). Then a random sample of population members  $\geq 122$  cm TL were transitioned to a recently harvested state and they were removed from the simulated population.

$$H_t \sim \text{Binomial}(Q_t, 0.875).$$

Note that simulation of the harvest management system over a time frame yields a set of stochastic results ( $Nh_t, yNh_t, H_t$ ) for any fixed set of starting conditions and parameters of the harvest policy function; therefore, evaluation of the policy function requires replication (size  $n$ ) of the model.

### ***Optimization***

The purpose of the optimization is to find the set of parameter values,  $\Theta_k \ni \{\alpha_k, \beta_k, Q_{\max_k}\}$ , for the logistic harvest policy function,  $\{Q_t\}$ , that best achieves management objectives. Alternative policies are candidate solutions to the optimization problem. Each alternative ( $k \in \{1, 2, \dots, K\}$ ) specifies a combination of parameter values  $\Theta_k$  that, in turn, defines a unique logistic function,  $\{Q_t\}_k$ . Alternative policies ( $k$ ) differ with respect to the combination of parameter values used in the policy function.

Any appropriate mathematical optimizer can be used to search for optimal solutions for the harvest policy function. I chose a genetic algorithm for its simplicity and broad availability. I defined the fitness measure being maximized within the algorithm to capture the dual objectives of maximizing cumulative long-term harvest and minimizing oscillations in population size. For

each simulated time series  $T$  years long, I calculated cumulative harvest ( $\Sigma H_{t_{H0}:T}$ ) and the range in total population size ( $N_{t,max} - N_{t,min}$ ) over the first fifty years with harvest ( $t = t_{H0}, t_{H0} + 1, \dots, T; T = 50$ ). Then, fitness for each candidate policy,  $k$ , was calculated by dividing the average cumulative harvest calculated from the set of stochastic replicates ( $n = 50$  per  $k$ ) by the average abundance range for the set. If abundance of harvestable alligators ( $Nh_t$ ) dropped below 100 in any of the 50 stochastic replicates for the policy  $\{Q_t\}_k$ , I stopped the simulation model and returned a fitness score of 0 for the policy. For policy  $k$ , the fitness score ( $Fitness_k$ ) is computed over years with harvest,  $t_{H0}$  ( $t = 51$ ) through  $T$  ( $t = 101$ ), and stochastic replicates  $j$  ( $n = 50$ ).

$$Fitness_k = \frac{\sum_{j=1}^n (\sum_{t=1}^T (H_{t,j}))}{\sum_{j=1}^n (N_{t,j,max} - N_{t,j,min})}$$

The algorithm begins with a population of  $K$  possible policy parameterizations,  $\Theta \ni \{\Theta_1, \Theta_2, \dots, \Theta_K\}$  that induce  $K$  possible policies  $\{Q_t\}_1, \{Q_t\}_2, \dots, \{Q_t\}_K$ . Values for each parameter in  $\Theta_k$  are randomly drawn from uniform distributions with parameter-specific search limits:  $\alpha$  (0, 0.07),  $\beta$  (0, 2000), and  $Q_{max}$  (100, 1000). I chose these limits based on results of early trials with the genetic algorithm that helped identify the ranges of values that were less likely to lead to a crash in the simulated alligator population before the designated end of the time series,  $T$ . I ran  $n = 50$  stochastic simulations for each policy alternative  $\{Q_t\}_k$  whereby management consequences were calculated for each alternative as if that alternative were to be implemented at every decision point, from the present into the future, over the course of the forward simulation. In other words, the policy function used to make management decisions was fixed over time within simulated time series. Each stochastic replicate was simulated over 101 ( $T$ ) discrete annual time steps with harvest beginning in year 51. At the beginning of each hunting season, the harvest

policy function  $\{Q_t\}_k$ , with parameter set  $\Theta_k$ , uses the most recent monitoring data ( $yNh_t$ ) to set the harvest quota,  $Q_t$ , for the upcoming hunting season.

The population simulation and management models described above were written and implemented in the program R version 4.0.3 (R Core Team 2021). I ran the optimization procedure in R version 4.0.4 (R Core Team 2021) using the genetic algorithm package (GA) 3.2.2 (Scrucca, 2013). I used a population of 200 alternative policies,  $\Theta_{1:K}$  where  $K = 200$ . I allowed the genetic algorithm to search for optimal solutions over 100 generations, or fewer if 50 generations elapsed without an improvement in fitness. Default values were used for the GA tuning parameters, including elitism (i.e., percent of top scoring policies in the current generation to retain without modification in the subsequent generation) = 5% ( $n = 10$  candidate policies), crossover probability = 0.8, and mutation probability = 0.1. The code used to implement the analysis is provided in Appendix F.

## Results

The genetic algorithm search ran for 96 generations (Figure 4.2). The parameter values ( $\Theta$ ) for the optimal policy function ( $\{Q\}^*$ ) were  $\alpha = 0.01077239$ ,  $\beta = 451.9207$ , and  $Q_{\max} = 278.8045$ . As a basis for comparison, population time series generated under the optimal harvest policy are plotted alongside population time series simulated under a static 13% proportional harvest rate. After the FFWCC's experimental harvest at Orange Lake, Woodward et al. (1992) concluded the alligator population could sustain a fixed harvest rate of 13% of harvestable size classes (subadult, adult, and bull) independent of sex. Policy  $\{Q\}^*$  received a fitness score of 9.2898 while the fitness of the populations simulated under a 13% proportional harvest policy was 3.238. Under the proportional harvest policy ( $\lambda = 13\%$ ), quotas are set at a fixed percentage

of subadult<sup>+</sup> counts ( $yN_h$ ). In contrast, harvest policy  $\{Q\}^*$  prescribes a state-based quota in accordance with the observed abundance of harvestable alligators (Figure 4.3).

Time series for populations simulated under different harvest policies diverge at the onset of harvest in year 51 ( $t_{H0}$ ), (Figure 4.4). Results here forward pertain to the last 50 years of the population time series ( $t = 51$  through 101; the first 50 years with harvest,  $t_{H0}: T$ ), which were used to compute fitness scores for policies in the GA. Under the no-harvest and  $\lambda$  policies, total abundance is relatively stable over years with harvest, whereas total abundance under policy  $\{Q\}^*$  declines over the first twenty years of harvest before it stabilizes with a smaller population size than the other two policies (Figure 4.4). It should be noted that the  $\lambda = 13\%$  policy was implemented following the same harvest management process as under  $\{Q\}^*$ . That is, the harvest probability (0.13) for sa<sup>+</sup> alligators each year was applied to the number of sa<sup>+</sup> alligators observed during annual count surveys ( $yN_h$ ), which is approximately 35% of the harvestable population. Then, due to partial controllability built into the harvest implementation process, annual take under the proportional harvest policy is closer to 4% annually.

Across all three harvest policy scenarios (no-harvest,  $\lambda$ , and  $\{Q\}^*$ ), there was an inverse relationship between alligator size and the variance of replicate abundances. The hatchling size class exhibited the greatest variability among stochastic replicates while deviations around mean abundances were lowest for the bull size class (Figure 4.5). Under scenario  $\{Q\}^*$ , juvenile, subadult and adult time series exhibit dampening oscillations over the first 30-40 years of harvest before appearing to stabilize (Figure 4.5). Time series for size class-specific abundances were similar under the proportional harvest ( $\lambda = 13\%$ ) and no-harvest policies ( $\lambda = 0\%$ ) (Figure 4.6). Annual abundances under the  $\lambda = 0\%$  and  $\lambda = 13\%$  policies were relatively stable from year-to-year and nearly equal with annual abundance typically being greater under the  $\lambda = 0\%$  policy

(Figure 4.6). Across size classes, oscillations are out of phase, reflecting the size class transition structure built into the model.

After fifty years of harvest, abundance of adult, bull, and hatchling size classes were consistently smaller under  $\{Q\}^*$  than under the  $\lambda = 0\%$  and  $13\%$  policies (Figure 4.6). Under  $\{Q\}^*$ , abundance in the subadult size classes declined over the first five years of harvest before it rebounding and exceeding subadult abundances under either of the other policies by year ten (Figure 4.6). After five years, the subadult population rebounded, growing to a maximum level before again dropping to the level of the earlier depressed abundance. After the first twenty years, subadult abundance continued to fluctuate but the magnitude of the oscillations decreased over time (Figure 4.6). After fifty years of harvest, subadult abundances were similar under all three policies (Figure 4.6). The juvenile size class was the only one to exhibit an increase in abundance at the onset of harvest under  $\{Q\}^*$ , but it was short-lived. After fifteen years of harvest, juvenile abundance under  $\{Q\}^*$  fell below juvenile abundance under either of the other policy scenarios and the pre-harvest abundance. During the second twenty-five years of harvest, juvenile abundance remained relatively stable at a level slightly lower level than the populations simulated under the  $\lambda$  and no-harvest scenarios (Figure 4.6).

The proportion of the population in each size class was roughly equivalent under the  $\lambda$  and no-harvest policies (Figure 4.7). After the first twenty-five years of harvest, size class distributions were similar in all three harvest policy scenarios (Figure 4.7). Under policy  $\{Q\}^*$ , the oscillations in abundance over the first 15-20 years of harvest shown in Figure 4.5 correspond with small fluctuations in the population's size class distribution (Figure 4.7). By the second 25 years of harvest, the size-class distribution stabilized and was similar to the populations under the  $\lambda$  and no-harvest policy with the exception of the non-harvestable size

classes (Figure 4.7). Relative to the  $\lambda$  and no-harvest policies, the stable size class distribution under the policy  $\{Q\}^*$  entailed a greater proportion of the population in the juvenile size class than the hatchling size class for most of the years with harvest (Figure 4.7).

Cumulative harvest ( $\sum H_{1:T}$ ) was greatest under the  $\{Q\}^*$  policy (Figure 4.8 and Figure 4.9). Total annual harvest ( $H_t$ ) was consistently (year-after-year) greater under  $\{Q\}^*$  than policy  $\lambda$ , and there was less inter-annual variability in total annual harvest under  $\{Q\}^*$  than  $\lambda$  (Figures 4.8, 4.9, and 4.10). However, annual abundances of harvestable (subadult<sup>+</sup>,  $N_{h_t}$ ) and adult<sup>+</sup> ( $N_{ad+,t}$ ) alligators were greater and more stable under the  $\lambda$  and no-harvest policies, especially over the first twenty-five years of harvest (Figures 4.8).

Under policy  $\{Q\}^*$ , the size class distribution of harvested alligators fluctuated some over the first twenty-five years of harvest as the proportion of harvest composed of subadults (hSA) versus adults (hA) oscillated (Figure 4.10). Once the size class distribution of harvest stabilized, in the second twenty-five years with harvest, a greater proportion of harvested alligators were subadults under policy  $\{Q\}^*$ , whereas adults and bulls made up a larger portion of annual harvest under policy  $\lambda$  (Figure 4.10).

## Discussion

This analysis demonstrates a way for alligator harvest managers to develop an optimal harvest policy for setting annual alligator hunt quotas based on population monitoring data. A logistic policy function parameterized with values that the genetic algorithm optimizer identified as optimal (i.e., the policy solution,  $\{Q\}^*$ ) better achieves the defined management objectives than the proportional harvest rate recommended by the FFWCC's experimental harvest study represented by policy  $\lambda = 13\%$ . Under policy  $\{Q\}^*$ , long-term harvests are maximized in balance

with population stability, although abundances fluctuate in the early years following the onset of harvest.

The demonstrated approach provides several advantages over existing agency practices. It is forward-looking, accounts for species biology and multiple sources of uncertainty, and provides population state-based decision guidance. It overcomes the ‘curse of dimensionality’ and is easily amendable to agency-specific objectives. The functional form of the fitness measure being optimized in the GA is flexible. Its shape can be adapted to fit other objective functions, allowing it to be tailored to specific agency needs.

The high dimensionality of the state-space required to capture alligator state transitions for optimization is troublesome for stochastic dynamic programming methods. Here, the computation of optimal harvest policies recognized size class transition dynamics. The size class transition structure built into the model produced dampening and asynchronous oscillations over the first several decades of harvest in juvenile, subadult, and adult size classes, which underscores the importance of a model that takes it into account. The search for an optimal harvest policy also accounted for multiple types of uncertainty - partial observability, partial controllability, and stochasticity - in the management system. Each year the observation process generated count data from the partially observed population of harvestable alligators ( $Nh_t$ ), which are the real target of management policies.

The results support the desired conclusion that the optimal policy solution from the GA ( $\{Q\}^*$ ) outperformed the constant proportional quota represented by the  $\lambda = 13\%$  policy, but the results were not computationally stable. The optimal policy search process was time consuming and required significant computer memory and processing capacity because fitness scores rested on the generation of replicate population time series for each policy option,  $k$ , using the

individual-based population simulation model. Fortunately, unlike dynamic programming methods, replicated simulation tasks and the genetic algorithm are both well-suited to parallelization. Therefore, to expedite the analysis, I ran the GA on a 36-core computer server in parallel using the built-in “parallel” argument in the `ga` function from the GA package in R (Scrucca, 2013). With parallelization activated, replicate population time series simulated under different candidate solutions in each generation of the GA population were generated on different computer processing units (CPUs) concurrently rather than on a single CPU consecutively. Despite specifying a random number generator (RNG) seed in the `ga` function and population simulation model, when population time series were simulated using the policy solution  $\{Q\}^*$  on a different computer, the fitness score differed from the fitness reported in the GA output. Fitness scores for other members of the population of candidate solution in the last generation of the GA, when calculated from time series simulated outside the GA changed, leading to a reordering of policy rankings. Thus, optimization results are not replicable on the machinery I used. Alternative optimizers or coding a special purpose GA may both be means to establish greater control over RNG behavior across multiple processors.

Computational concerns aside, drawing the desired conclusion from the optimization presented in this chapter requires several assumptions be satisfied. First, simulation models must be good representations of the management system. This means management system sub-models (i.e., the population, observation, and harvest models) are consistent with reality. For example, the stochastic observation and harvest implementation models assume detection probability and harvest probability, 0.35 and 0.875, respectively, are static through time. A detection probability of 0.35 may be optimistic. It would be useful to run the optimization with different detection probabilities used in the observation process model to show the sensitivity of the optimal policy.

A reasonable hypothesis would expect policies to become increasingly conservative as detection probability decreases. Such a scenario suggests a tradeoff between monitoring effort and opportunity costs although the effect would depend on the level of sensitivity.

Another requisite assumption is that all sources of mortality are captured in the population model. In some states, agencies administer multiple alligator management programs, e.g., for harvest on private lands, nuisance control, and egg or hatchling collection. In places where multiple harvest programs operate, decision making for each one is independent from the others. If alligators are being removed from the population through co-occurring management programs, they need to be accounted for in the system model for the policy solution to produce the expected optimal outcomes.

The results may be vulnerable to several types of bias: selection, measurement, and confounding. My decision to use the `ga` function from the `GA` package in R may have contributed to the results of this analysis. There are other ways to run a genetic algorithm as well as other optimizer options altogether. The key to ADP is a system process model that can be used for forward simulation. Another possible source of selection bias was my choice of a logistic policy function; the harvest policy can have other functional forms.

The optimal policy is sensitive to the choice of fitness function. Another requisite assumption is that the fitness function accurately measures management objectives. The policy solution is only optimal given the objective function optimized in the search process. The fitness function described in the Methods section was intended to reward policies that maximized cumulative harvest over fifty years while penalizing policies that led to instability in abundances. After additional consideration, I believe fitness should have been computed differently. Instead of what was used, the fitness score assigned to each candidate solution should have been

calculated by first computing the ratio of cumulative harvest to the range in abundances ( $\Sigma H / (N_{max} - N_{min})$ ) for each time series replicate, then calculating average of replicate fitness scores (i.e., reverse the ordering of summation and division).

The parameter set  $\Theta$  identified as the optimal policy solution changed when fitness scores were calculated using longer time series, e.g., 100 years after harvest initiated instead of 50. Changing the number of replicate population time series simulated under each GA candidate solution also affected fitness scores and ranking of candidate policy solutions. Other potential sources of bias include the size of the GA population of candidate solutions and the length of the search process (i.e., number of generations). Additionally, bias may be introduced through the GA tuning parameter settings, e.g., crossover and mutation probabilities, or any other constraints imposed on the search process, such as setting the run argument to exit the GA if fifty consecutive generations elapsed without an improvement in fitness.

Possible sources of measurement bias include the choice of fitness equation variables, their relations, and choice of records selected for calculation. The implementation of the fitness calculation (i.e., its definition in code) warrants careful consideration. As mentioned earlier, a more appropriate expression of fitness would involve averaging replicates of the ratios of cumulative harvest to population range.

Future applications of this approach may consider size-structured harvest policies informed by size-structured monitoring data; however, accounting for the increase in observational uncertainty may likely offset any hoped-for performance gains of fine scale management. The optimization could also be revised to account for parametric uncertainty in the population model by providing posterior distributions of parameters to the forward simulation model. However, given the long time required to run the analysis as it is, accounting for

parametric uncertainty would require simplifications in other parts of the model, if computational efficiencies cannot be found.

Table 4.1

*Chapter 4 Notation*

Notation	Description
$yNh_t$	annual monitoring data input for optimizer; number of harvestable alligators ( $\geq 122$ cm TL) in year $t$ ; $yNh_t \sim \text{Binomial}(Nh_t, 0.35)$ , where 0.35 was based on the proportion of harvestable alligators observed on the survey route during average August water temperatures ( $31^\circ$ C) (Woodward et al., 1992)
$Q_t$	harvest quota (in number of alligators $\geq 122$ cm TL) for year $t$ ; intended hunting season outcomes
$\alpha$	slope, or rate of change (steepness), of curve at the inflection point
$\beta$	value on x-axis at inflection point of the sigmoid curve
$Q_{max}$	maximum allowable annual take
$\eta$	harvest factor on logit scale
$\Theta_k$	parameter set $k$ with harvest policy function parameters $\alpha_k$ , $\beta_k$ , and $Q_{max,k}$
$\{Q_t\}$	logistic harvest policy function that produces a quota for year $t$
$\{Q_t\}_k$	logistic harvest policy function with the parameter values in set $\Theta_k$
$\{Q\}^*$	optimal harvest policy identified by the genetic algorithm
$H_t$	total annual harvest; actual hunting season outcomes

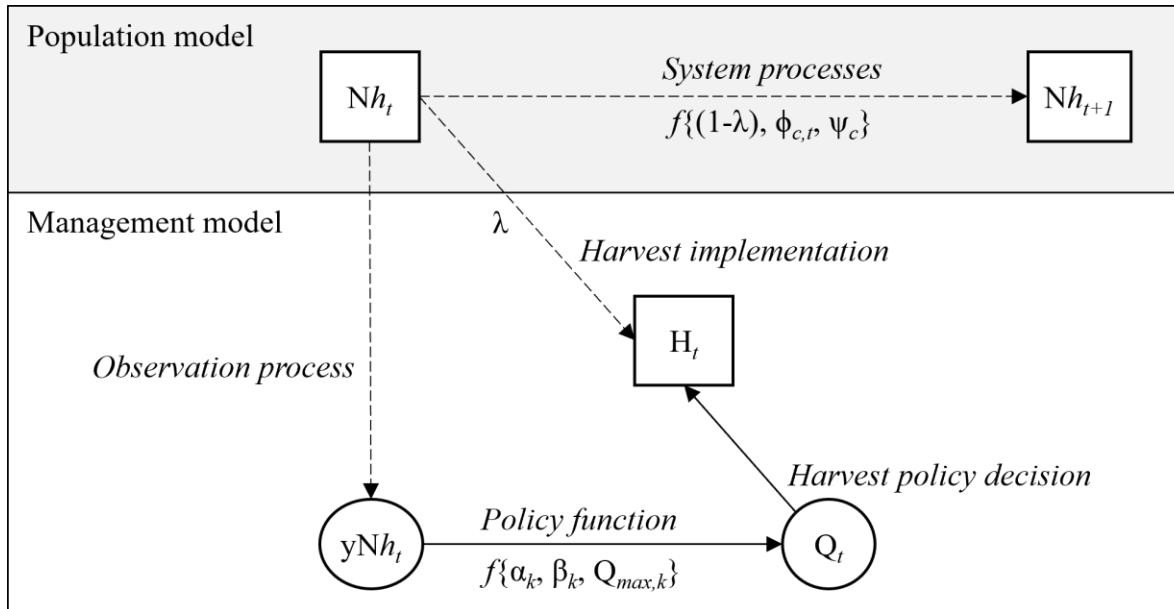
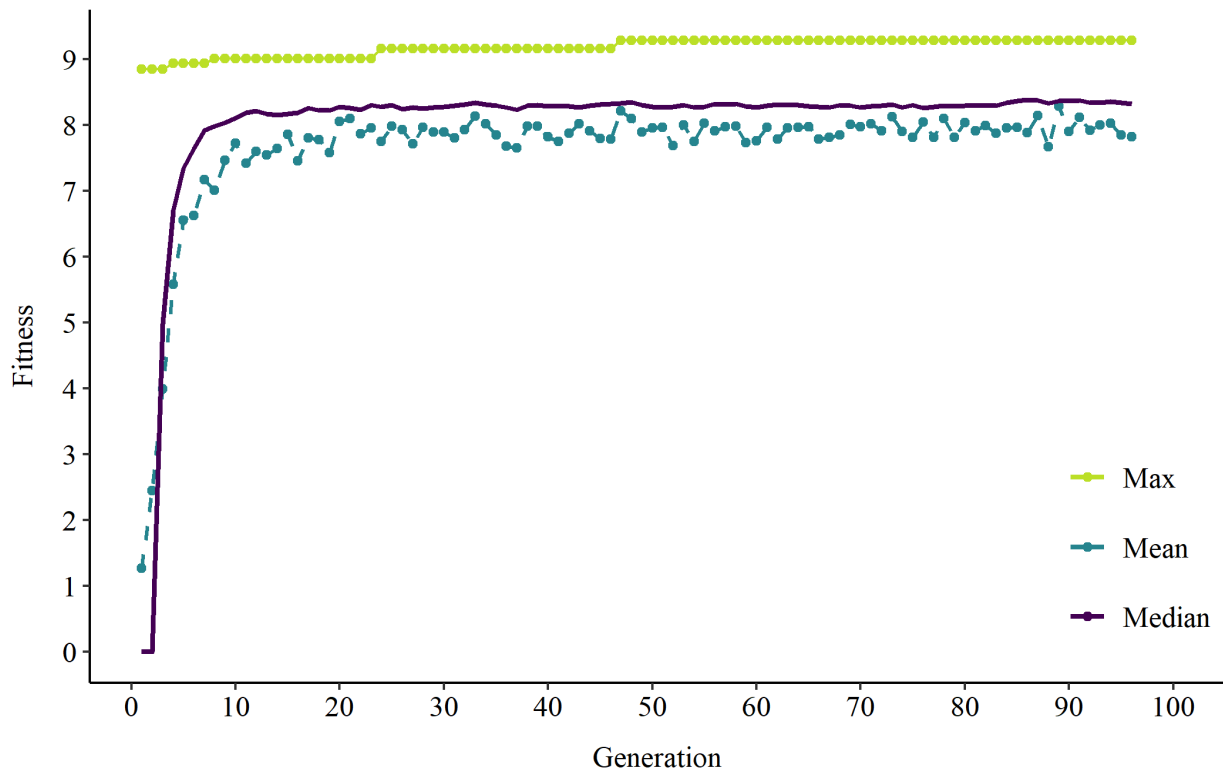


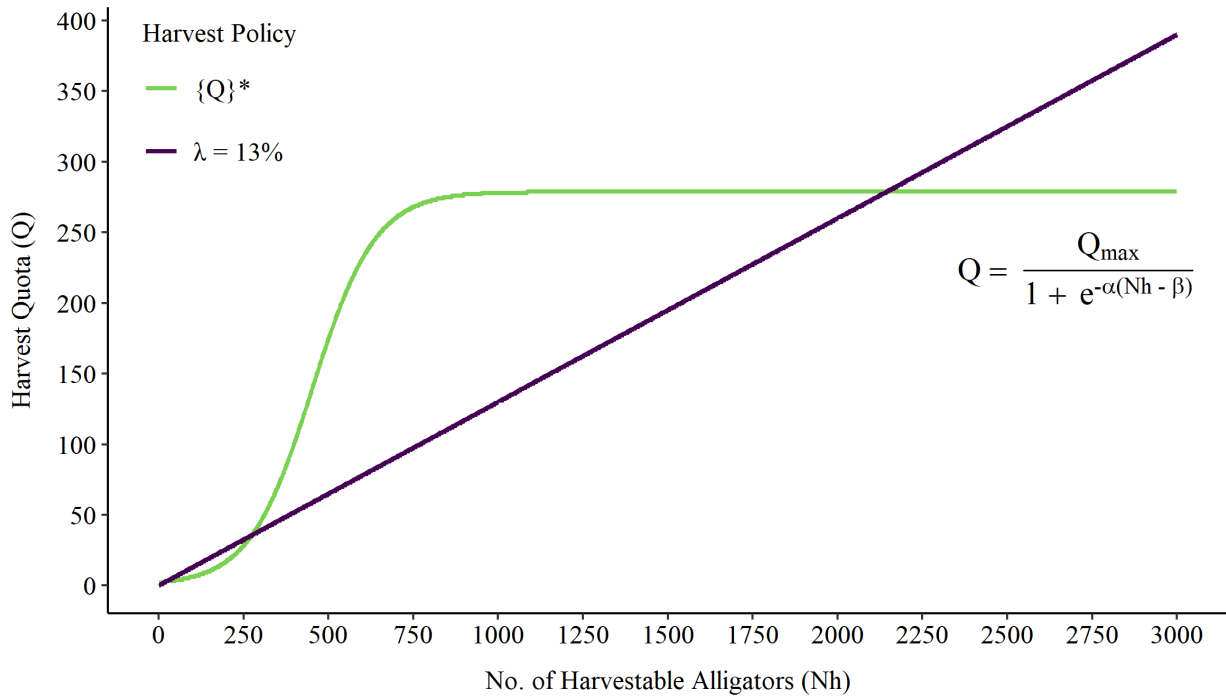
Figure 4.1 Simulated Alligator Harvest Management System

Components of the alligator harvest management system simulated in the optimization procedure. The population model (gray shaded rectangle) describes the system processes responsible for annual state transitions for harvestable alligators ( $\geq 122$  cm TL,  $Nh_t$  to  $Nh_{t+1}$ ). Annual population change results from demographic processes, including survival through the hunting season ( $1-\lambda_t$ ), survival outside of hunting season ( $\phi_{c,t}$ ), and growth, which advances some individuals to the next larger size class ( $\psi_{c,t}$ ). The management model is implemented at the beginning of the annual timestep ( $t$ ) over the period  $t = \{t_{H0}, t_{H0} + 1, \dots, T\}$  through a sequence of limited duration annual harvest quotas. Prior to each hunting season, an observation process partially observes the state of the harvestable population ( $Nh_t$ ) as recorded in count data ( $yNh_t$ ). Then, policy function  $k$  defined by the parameters  $\alpha_k$ ,  $\beta_k$ , and  $Q_{max,k}$  uses  $yNh_t$  to set the harvest quota for the upcoming hunting season,  $Q_t$ . Then the quota is imperfectly realized during harvest implementation resulting in the total harvest for year  $t$ ,  $H_t$ .



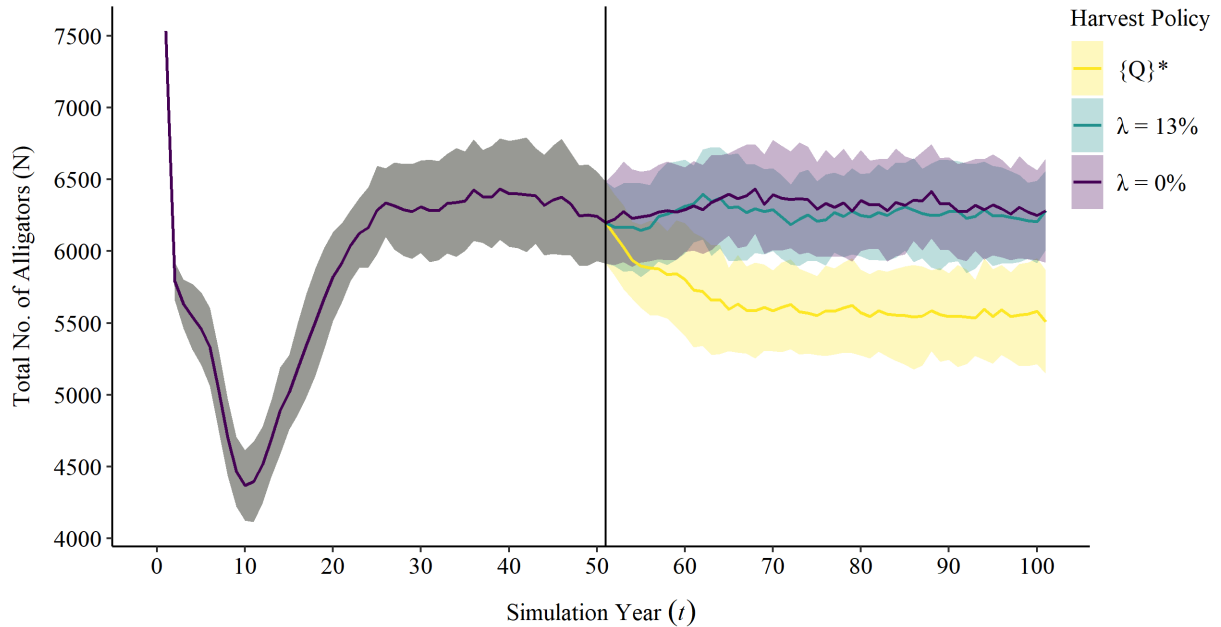
*Figure 4.2* Evolution of Population Fitness Scores during the Genetic Algorithm Search for an Optimal Harvest Policy Solution

Best (max), mean and median fitness values computed for the population of candidate policy solutions ( $N = 200$ ) in each generation of the genetic algorithm (GA) search process. The GA search ended after 96 generations following a period of 50 consecutive generations without an improvement in fitness.



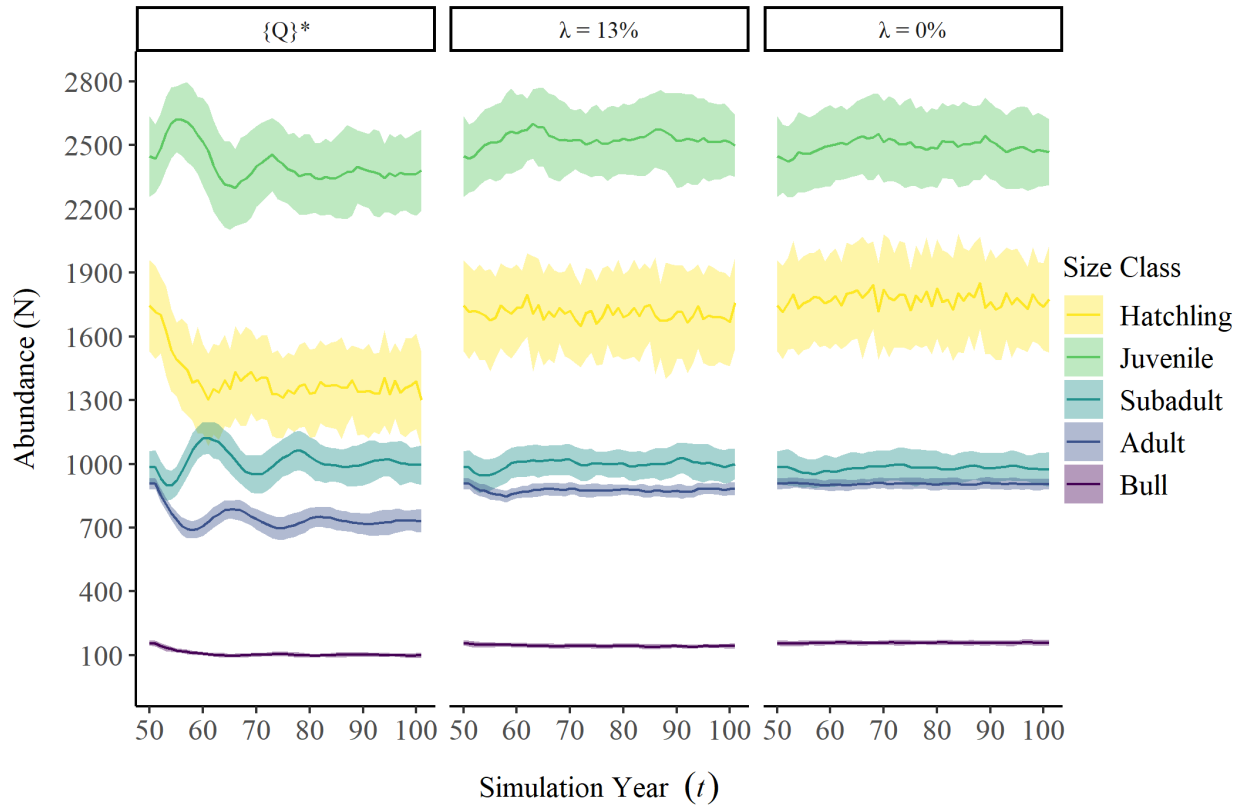
*Figure 4.3* Comparison of Harvest Policy Functions

Comparison of harvest policy functions used to translate abundance of subadult<sup>+</sup> alligators (Nh) into a harvest quota (Q) for the annual alligator hunting season. The green logistic curve depicts the optimal policy identified by the optimization procedure ( $\{Q\}^*$ ) with parameters  $\alpha$  (0.01077239),  $\beta$  (451.9207), and  $Q_{\max}$  (278.8045). The linear function in purple depicts a 13% proportional harvest rate ( $\lambda = 13\%$ ) for subadult<sup>+</sup> alligators. To clarify, in the alligator population simulation model, the annual hunting quota ( $Q_t$ ) under policy  $\{Q\}^*$  depends on imperfect observations of  $Nh_t$  in the form of count survey data ( $yNh_t$ ), not the true latent abundance,  $Nh$ , depicted above.



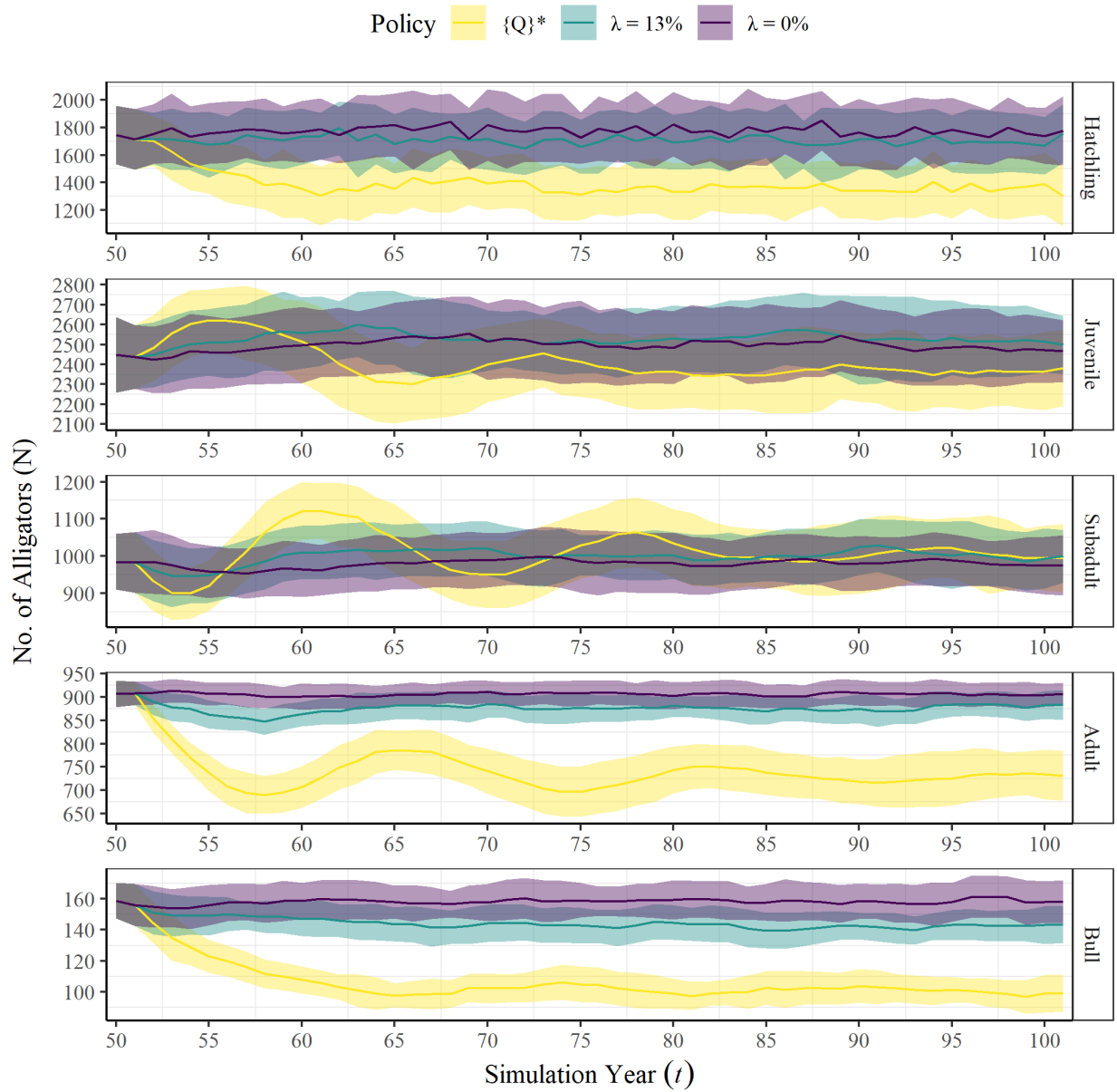
*Figure 4.4* Total Alligator Abundance Under Different Harvest Policies

Total number of individuals (N) in the simulated alligator population over one-hundred annual time steps ( $t$ ) under alternative harvest policy scenarios. Annual harvest of subadult<sup>+</sup> alligators ( $\geq 122$  cm TL) begins in year 51 (dotted vertical line) under the optimal harvest policy  $\{Q\}^*$  identified by the genetic algorithm (yellow) or under a 13% proportional harvest quota ( $\lambda = 13\%$ ). A no-harvest scenario ( $\lambda = 0\%$ ; purple) provides a basis for comparison with a population that is never subjected to harvest. Solid colored lines mark the annual mean value for fifty stochastic replicate simulations with shaded ribbons around the means marking  $\pm 1$  SD.

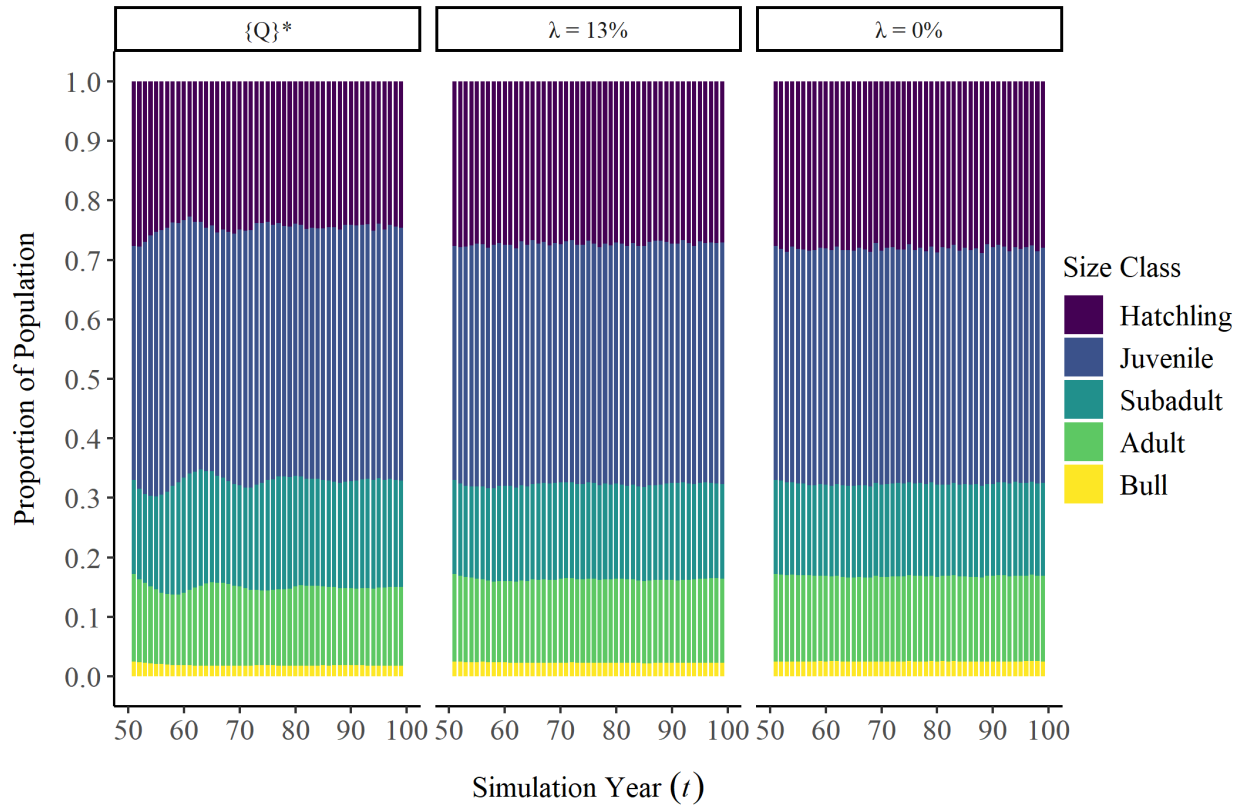


*Figure 4.5* Comparison of Annual Alligator Size Class Abundances Under Different Harvest Policies

Harvest policies include:  $\{Q\}^*$  uses the optimal policy identified by the genetic algorithm to set the annual hunt quota;  $\lambda = 13\%$  subjects the harvestable population to a constant annual harvest rate each year; and a no-harvest policy ( $\lambda = 0\%$ ) provides a basis for comparison. Solid colored lines mark the annual mean value from fifty stochastic replicate simulations and adjacent colored ribbons cover  $\pm 1$  SD from the mean.

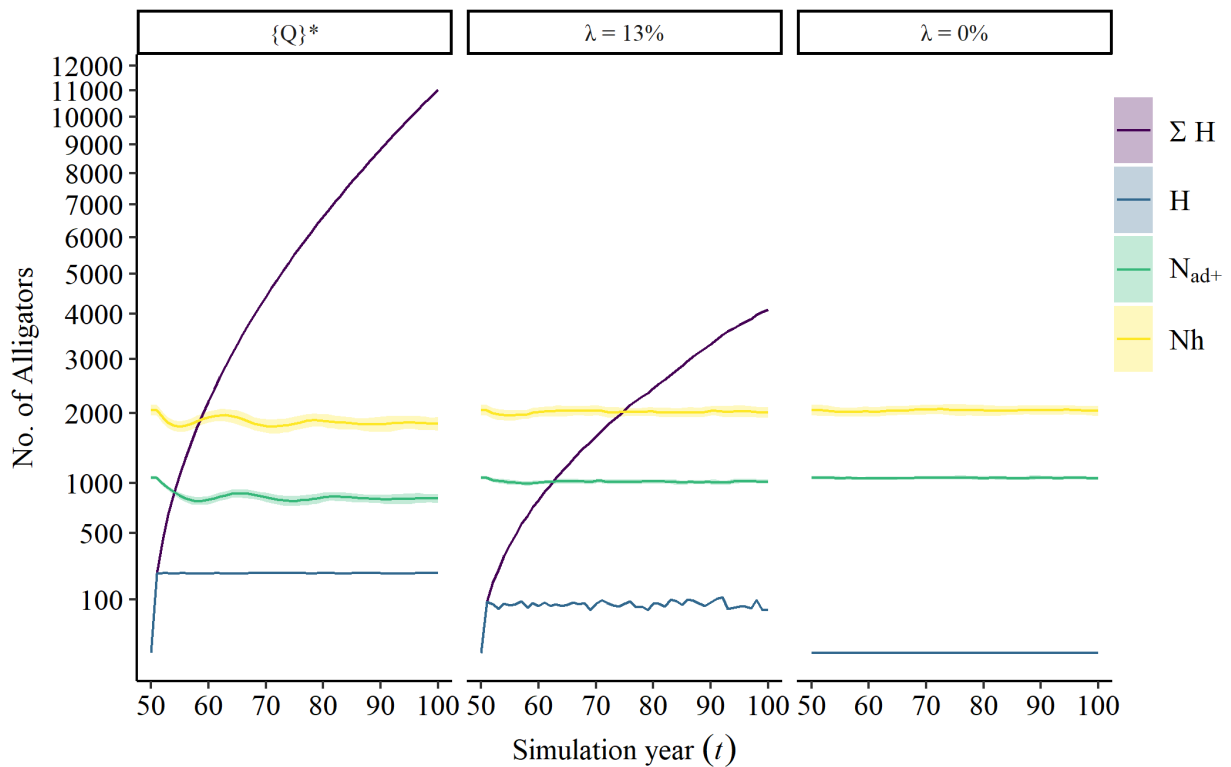


*Figure 4.6* Abundance Time Series Simulated Under Different Harvest Policies by Size Class  
 Harvest policies include:  $\{Q\}^*$  uses the optimal policy identified by the genetic algorithm to set the annual hunt quota (yellow);  $\lambda = 13\%$  subjects the harvestable population to a constant annual harvest rate each year (turquoise); and a no-harvest policy ( $\lambda = 0\%$ ) provides a basis for comparison (purple). Solid colored lines mark the annual mean value from fifty stochastic replicate simulations and adjacent colored ribbons cover  $\pm 1$  SD from the mean.



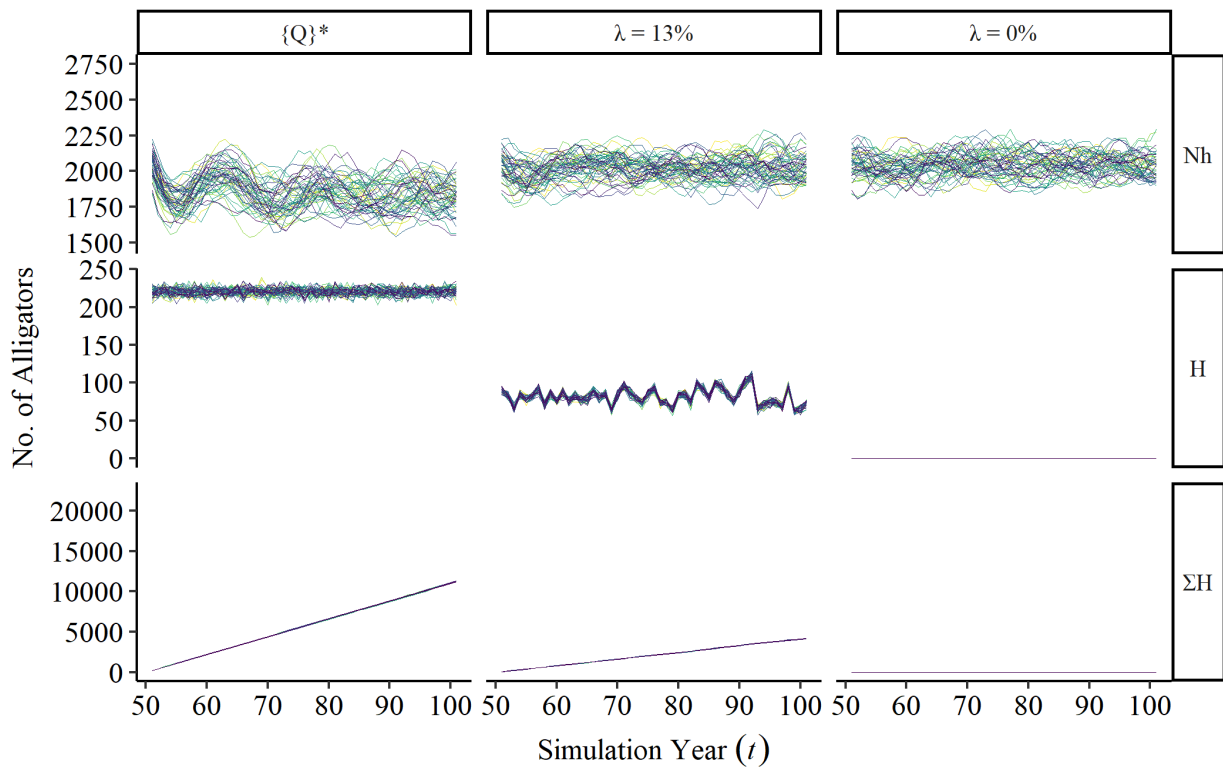
*Figure 4.7* Comparison of Annual Alligator Size Class Distributions Under Alternative Harvest Policies

Size class distributions over the 50-year period used to compute fitness in the genetic algorithm under three alternative policies:  $\{Q\}^*$  uses the optimal policy identified by the genetic algorithm to set the hunt quota each year;  $\lambda = 13\%$  subjects the harvestable population to the same proportional harvest rate (0.13) each year; and a no-harvest policy ( $\lambda = 0\%$ ) provides a basis for comparison.



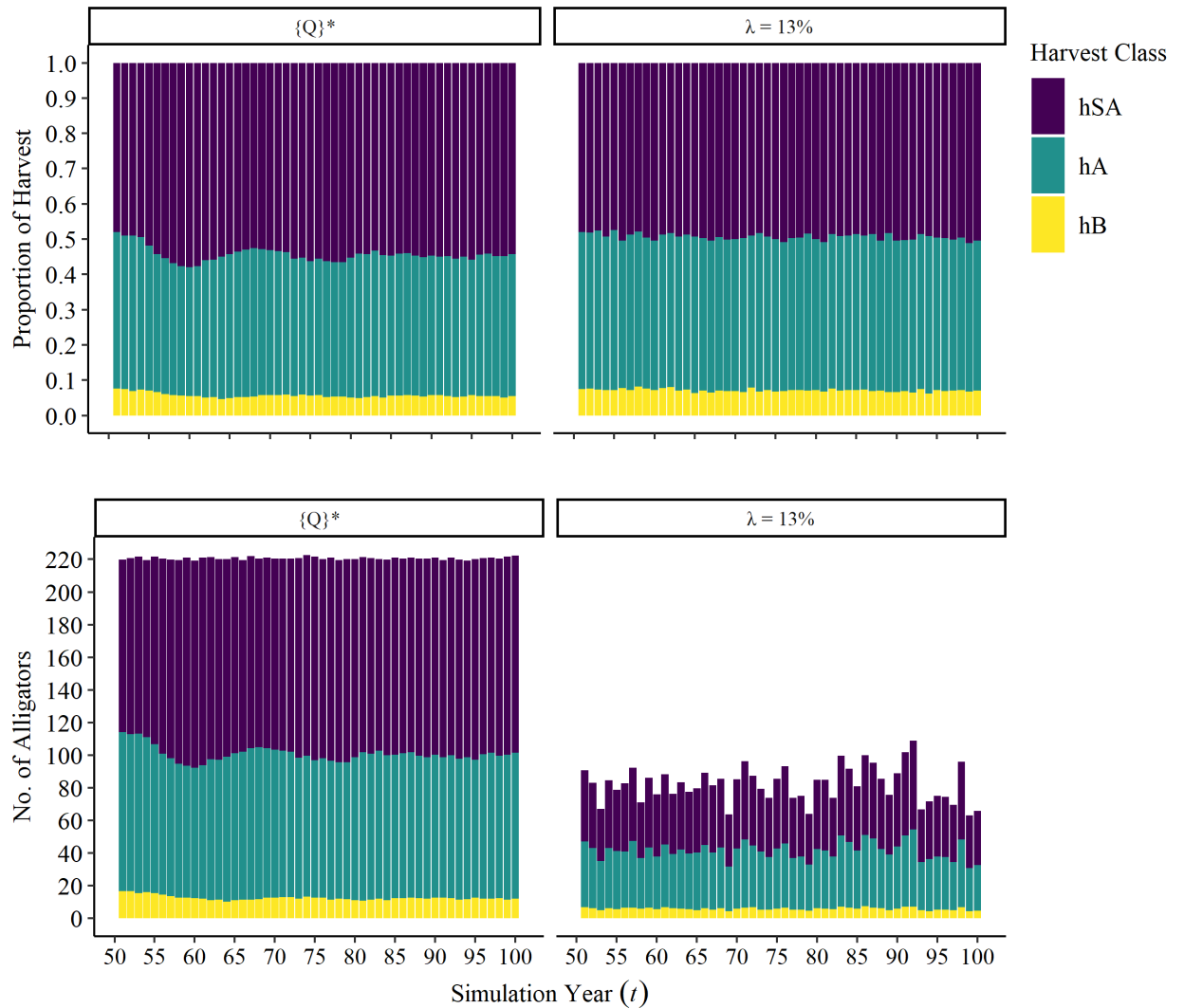
*Figure 4.8* Comparison of Population Harvest Outcomes Under Alternative Management Policies

Comparison of population time series generated under different harvest policies: the optimal policy identified by the genetic algorithm ( $\{Q\}^*$ ), a constant harvest rate policy ( $\lambda = 13\%$ ), and a no-harvest policy ( $\lambda = 0\%$ ). Plotted lines show the mean square root of annual abundance  $\pm 1$  SD computed from fifty stochastic replicate simulations for the following state variables: cumulative total harvest ( $\Sigma H$ ), total annual harvest ( $H$ ), annual abundance of the adult<sup>+</sup> ( $N_{ad+}$ ) and subadult<sup>+</sup> ( $N_h$ ) population at the beginning of the hunting season. Both harvest policies,  $\{Q\}^*$  and  $\lambda = 13\%$ , set the annual harvest quota based on the number of harvestable alligators observed during monitoring surveys (i.e. recorded in count data), not latent abundance ( $N_h$ ).



*Figure 4.9* Comparison of Harvest Time Series Generated Under Different Policy Scenarios

Time series for harvest-related variables (cumulative total harvest,  $\Sigma H$ ; total annual harvest,  $H$ ; and annual abundance of the subadult<sup>+</sup> population at the beginning of the hunting season,  $N_h$ ) from fifty stochastic replicates simulated under each harvest policy scenario: the optimal policy identified by the genetic algorithm ( $\{Q\}^*$ ), a proportional harvest rate policy ( $\lambda = 13\%$ ), and a no-harvest policy ( $\lambda = 0\%$ ) scenario.



*Figure 4.10* Annual Harvest Outcomes by Size Class Under Alternative Harvest Policies

Annual harvest outcomes generated by alternative harvest policies: the optimal policy identified by the genetic algorithm ( $\{Q\}^*$ ) and a constant harvest rate policy ( $\lambda = 13\%$ ). Data shown are mean values computed from fifty stochastic replicate simulated time series. The top row shows the size class distribution of the total annual harvest, and the bottom row presents the distribution of the total harvest by the number of alligators in each harvestable size class: subadult (hSA), adult (hA), and bull (hB).

## CHAPTER 5

### **Relational Power in Natural Resource Management Applications of Structured Decision**

#### **Making: An Autoethnography**

The government institutions responsible for fish and wildlife resources in the United States emerged around the turn of the twentieth century in a particular social context when top-down governance by experts was standard (Jacobson & Decker, 2006). Legislative and regulatory authority remains with federal and state resource management agencies (agencies) though the social context in many places changed over time. Preserving agency relevancy and legitimacy requires new approaches to environmental governance (Jacobson & Decker, 2008; Sullivan et al., 2022). Stakeholders today demand efficiency, transparency, accountability, and inclusiveness from agencies in conservation decision-making (Runge et al., 2013).

In the 1990s, researchers within the U.S. Geological Survey (USGS) and U.S. Fish and Wildlife Service (USFWS) began using structured decision making (SDM) in environmental management contexts at federal, state, and local levels nationwide (Fuller et al., 2020). Structured decision making (SDM) is an iterative process of decision structuring and analysis that developed in the business sector before its adoption by fish and wildlife management professionals (Gregory et al., 2012). The USFWS now uses structured decision making across administrative branches and offers training courses in SDM and related tools for employees and professionals from other Department of the Interior (DOI) agencies (National Conservation Training Center & U.S. Fish and Wildlife Service, 2014).

Formal application of SDM reportedly facilitates transparent accounting of the moral, legal, and social responsibilities of those involved in a particular decision context (Brignon et al., 2019). SDM provides a framework for introducing, managing, negotiating, and applying data, in conjunction with expert opinion and subjective preferences in the process of framing decisions, evaluating alternative decision options, and assessing uncertainty (Nichols et al., 2015). In environmental management contexts, the essential components of the SDM process, known by the acronym PrOACT, include a detailed statement of the decision problem, an explicit statement of the decision maker's desired outcomes (objectives), the identification of potential management actions (alternatives), development of predictive models to forecast system responses to management alternatives (consequences), assessment of the probability of predicted consequences and specifying preferences for predicted consequences, then comparisons among alternatives to identify tradeoffs (tradeoffs), and establishment of a monitoring program to estimate the state of the system at each decision point and other variables relevant for decision making (Keeney, 1982; Nichols et al., 2007).

My introduction to SDM began when I was hired for a graduate research assistantship through the Georgia Cooperative Fish and Wildlife Research Unit (GA Coop Unit) in the Warnell School of Forestry and Natural Resources (Warnell) at the University of Georgia (UGA). Cooperative Fish and Wildlife Research Units (Coop Unit(s)) are land grant university-hosted entities co-owned by the university, the state government's fish and wildlife agency, and USGS that serve the research and technical assistance needs of state cooperators. My project focused on developing a decision-making framework prototype for alligator harvest management programs in the species' eastern range based on the principles of decision analysis. Specifically, I worked on two deliverables: (1) an alligator harvest model for predicting population responses to

hunting pressure under different management scenarios; and (2) a framework for setting annual alligator harvest quotas according to population consequences predicted by the alligator harvest model and consideration of tradeoffs among coexisting management objectives. As one of many similar graduate student assistantships offered through Coop Units over the last decade, my project exemplifies the ongoing campaign by DOI professionals, primarily within USGS and the USFWS, to advance SDM and decision-theoretic approaches to adaptive resource management (AM) in fish and wildlife management contexts. At least twelve universities with Coop Units now offer nature resource decision-making courses for undergraduate and graduate wildlife programs to teach decision science methods skills to future wildlife researchers and managers (Fuller et al., 2020). I was a teaching assistant for one of these courses at Warnell called Conservation Decision Making.

At the start of my graduate assistantship, my advisor and I met face-to-face with the alligator managers from the wildlife management agencies in Alabama, Florida, Georgia, and South Carolina to learn about existing approaches to alligator harvest management decision making and agencies' decision-support needs. We primarily interacted with the wildlife professionals responsible for day-to-day population monitoring and harvest program management. As I started to engage in practice, my experiences brought out power dimensions that I previously overlooked or under appreciated.

The importance of power dynamics in conservation was not a foreign concept to me before working on the alligator harvest decision-support project. However, working previously in more traditional scientific research settings to generate biological knowledge, I rarely, if ever, considered the power dimensions of my work. In my naivete I believed my influence in conservation contexts depended most on the sincerity of my intentions, adherence to personal

and professional ethics, practiced with humility, confidence, respect for others, patience, and persistence.

The power dimensions of my work became apparent to me as I advanced through my program of study in the Integrative Conservation (ICON) doctoral program at UGA. The ICON curriculum illuminates alternative perspectives that bear on the concepts, assumptions, and ways of discerning tradeoffs inherent to the complex systems in which conservation occurs (Advancing Conservation in a Social Context (ACSC), 2011; McShane et al., 2011). Engaging with unfamiliar philosophical perspectives and scholarship produced by researchers with different epistemologies sparked my curiosity regarding interrelationships between knowledge and power in SDM applications. I began questioning and reflecting on the professional relations established by SDM practitioners and how power disparities enable and constrain participants' contributions. In environmental governance, power determines "what is known, what is emphasized, and who prevails" (Brisbois & de Loë, 2016).

In participatory decision-making processes, who is engaged, when, and in what capacity affects the quality of decisions produced (Reed, 2008). The role and responsibility of individuals and organizational participants influences knowledge production processes, particularly the integration of co-generated knowledge (Lawrence, 2015; Rosendahl et al., 2015). Published examples of the SDM frameworks developed for multi-objective resource management problems tend to focus on the stages of the decision structuring and analysis process, and content of the decision framework that was produced, often with minimal information about the role of participant relations in interagency SDM applications.

In the remainder of this chapter, I aim to complement SDM scholarship by offering a novel perspective on SDM approaches to environmental management informed by theories of

relational power. To demonstrate how practitioners' socially structured (professional) relations co-construct collaborative SDM applications, I present examples from my lived experience. I intend to illuminate how individual and institutional relations shape SDM practice as well as its portrayal in the peer-reviewed literature by considering SDM through the lens of socially structured power disparities.

### **Autoethnography: A Process and Product**

My primary source of analysis is my own experience and perceptions of events during my doctoral program (2013 – 2018): (1) a series of meetings with state agency staff to collect information related to my alligator research, (2) my role as a participant observer of SDM workshops, and (3) my role as an active participant in an SDM workshop. I use autoethnography to examine and share insights from my experience developing analytical solutions for science-based alligator harvest management programs and observing teams of wildlife professionals developing a rapid prototype SDM framework. Analytical and interpretive in form, my autoethnography provides a venue for reflexivity, a critical component of integrative conservation research (IR). Reflexivity creates space for critical examination of a researcher's own positionality with respect to their engagement in, and in relation, to the socio-ecological systems they study, thereby acknowledging the intrinsic role of power in environmental knowledge production. I draw from my graduate assistantship work with alligator harvest program managers and participant observation of four inter-agency teams I observed at structured decision-making workshops hosted by the USFWS's National Conservation Training Center (NCTC) in Shepherdstown, West Virginia. SDM workshops at NCTC are foundational to applications of decision science across North America. Many published SDM case studies originated from, or developed at, one of these workshops.

SDM workshops at NCTC are training courses, which use a learning-while-doing, or “experiential”, teaching model. During the week-long workshop, participants learn the SDM process while being coached to develop a decision framework to address a real-world problem for which they found traditional approaches insufficient. As teams develop a prototype for their local application, the workshops simultaneously augment agency capacity in SDM expertise. Since 2006, over one-hundred workshop teams completed the week-long course. Together, NCTC and SDM practitioners developed applications of SDM to help USFWS decision makers make real decisions for fish and wildlife management, e.g., regarding endangered species, migratory birds, and regional-scale refuge management.

Workshop teams’ motivations for attending the workshop vary in ways that influence their experience. Along with addressing different decision problems, workshop teams differ with regards to the outcomes they cared most about. Of the teams I observed, some participated primarily for the professional development opportunity (i.e., to learn the process for use in the future). A management urgency motivated others to attend for the opportunity to be led through the process by a respected expert; for example, assessment of near-term conservation measures required to maintain an endangered species on the landscape long enough for longer-term land management measures to produce habitat characteristics required for species persistence.

Differences in teams’ underlying interest in the workshop were apparent in the specificity and durability of team problem definitions. Defining the decision problem is the first stage of the SDM process. When team coordinators submit their team decision problem proposal to workshop organizers, they provide a general description of the problem the team wants to address. Once teams are selected, the team coordinator and their coaching team with whom they are matched are instructed to refine the decision problem and arrive at the workshop with a more

developed problem statement. At the beginning of the week, team problem statements were variably developed, and they evolved to different extents by the end of the week, in some cases being revised to address a different problem after team discussions clarifies team members concerns or capacity.

My own experiences at SDM workshops offered through NCTC inform my understanding of the workshops. In 2015, I attended my first SDM workshop at NCTC as an observer. Observers are workshop participants who are not associated with a particular case study team but are interested in seeing the SDM process in action, often with the intention to later facilitate teams themselves. During the workshop, observers move among team rooms to experience different types of applications and coaching styles. In 2018, I attended my second NCTC SDM workshop where I co-coached a team. I was matched with the team after replying to a call for coaches on the USFWS-SDM listserv, which I joined after the workshop in 2015. Unlike the February 2015 workshop that I attended on the NCTC campus in Shepherdstown, WV, the July 2018 workshop was held off-campus in Gainesville, FL, at a site organized by NCTC and local USGS researchers, who were also coordinators of one of the participating teams. At this workshop, there were four teams from across the southeast, each focused on a reptile or amphibian species of concern, but decision problems varied from coordinating trapping efforts for an invasive species across south FL, to deciding whether a captive breeding program should be established for an endangered species. Because I was a team co-coach at the 2018 workshop, I only observed my team's interactions before and during the 2018 workshop.

Information I recorded at workshops and meetings throughout my doctoral program provided me with ample content for writing an autoethnography. Throughout my doctoral program, I routinely made notes, kept digital and hand-written records, saved email

correspondence, and collected artifacts related to my professional activities, which constitute the basis of this chapter. When possible, I consulted NCTC SDM team white papers developed from the workshops. Within sixty days of the workshop, the team coordinator is expected to submit a five to eight-page white paper summary of their team's decision framework with a discussion of the team's workshop experience using a template provided by NCTC. I also triangulated information from my notes with published reports and peer-reviewed journal articles, state and federal management agency websites, online training materials, and conversations with practitioners (i.e., colleagues and collaborators, e.g., at conferences, workshops, and other professional gatherings).

### **Relational Power**

Power dynamics are fundamental elements of conservation research and practice that have important policy implications (Shackleton et al. 2022). Because research conducted by conservation scientists determines which uncertainties are recognized, how they are addressed, and what information is shared, with whom and how, it is an expression of authority. Through its contributions to policy narratives, conservation research wields power over how policy issues come to be known (Hirsch et al., 2010). Thus, the agencies structuring and defending their actions through SDM empower it as a way of knowing conservation policy issues (Feldman et al., 2006).

Power of individuals (sometimes referred to as actors or agents) and institutions varies socially, among contexts based on individuals' roles, positions in organizational hierarchies, and relationships with other actors and their social structures. The realist theory of power recognizes actors' multiple and mobile relations, which helps identify the enduring structural preconditions that shape contingent human interaction (Raik et al., 2008). Relationships between the agency of

individuals (i.e., ability to act, express power) and the social structures in which they are embedded reveal the workings of power (Raik et al., 2008). Standpoint theory recognizes how individuals occupying a specific social position in a group of participants can simultaneously facilitate or hinder their understanding and options for action (Harding, 2004, pp. 1–15). Socially structured relationships, such as roles on a team, create power disparities among conservation collaborators and partners. For this paper, I use the term power to refer to the capability to alter another's behavior, broadly interpreted here as in social science to include cognition and affect (Gaski, 2020), and the concept of social power describes the ability of actors to directly influence outcomes (Boonstra, 2016).

I use a realist perspective to examine power relations among the actors and institutions using SDM in environmental governance. From a realist perspective, social structures constrain and enable human agency, which reinforces or restructures social relationships. Therefore, power is the capacity to act within preconditioned structured social relations (Raik et al., 2008). This perspective makes it possible to study agents (e.g., SDM practitioners and process participants) and the socially structured relations in which they interact (e.g., while engaged in process, in training/learning contexts, as a professional within a field/community of practice), as well as how the two conspire to empower or constrain individual and organizational agency. The practical value of the realist perspective is that by understanding agents' participation in different social structures, we can envision how they might transform them for better or worse outcomes (Raik et al., 2008).

Many definitions, descriptions, and classifications of power exist in the peer-reviewed literature, within and across intellectual fields (Gaski, 2020). Below, I present my insights regarding hidden power dynamics based on the conceptual framework developed for

collaborative water governance initiatives by Brisbois and de Loë (2016). The framework encompasses overlapping instrumental, structural, and discursive dimensions of the ways "A exercises power over B" originally proposed by Lukes (2005). Instrumental power derives from the resources, physical or capital, that an actor may use to shape policy outcomes in competition with others. Instrumental power is, perhaps, the most easily recognized dimension of power given its visibility. An actor's ability to shape policy agendas is known as structural power (Brisbois & de Loë, 2016). Structural power determines how problems are framed and which items make it on the agenda. It actively or implicitly controls who may participate and who may not, and it controls which information is deemed credible and how knowledge will be gathered and applied. Some expressions of structural power are visible while others are not (Brisbois & de Loë, 2016). The third dimension of power, discursive power, describes the ability to influence the wants and desires of others (Brisbois & de Loë, 2016). Discursive power may be subtle but tends to be strong among actors with significant structural and instrumental power (Brisbois & de Loë, 2016).

Power may emerge from material or ideational sources. Ideational sources arise from social constructs such as ideas, norms, and values, including perceptions of actors as legitimate, knowledgeable, or trustworthy, or as possessing authority (Fritz & Binder, 2020). Ideational sources provide opportunities for actors to increase their power relative to others their significance in a particular context is relative (Fritz & Binder, 2020). Material sources of power include such things as funding or access to natural or technological assets (e.g., communication infrastructure), which may be associated with structural conditions or belong to specific actors. In structural contexts that provide direct rule-setting or regulatory power, material sources enable actors to set agendas and make decisions.

In the Findings section that follows, I describe key roles on SDM workshop teams – coaches, team coordinators and decision makers. Then, I identify the types of agents and institutions filling these roles and I discuss connections between participants’ engagement in collaborative SDM applications, their socially structured relations and involvement in SDM practice and environmental governance beyond individual applications of SDM, and power. In the Reflection and Discussion section after that, I discuss my own role in, and in relation to, SDM practice, and I discuss how my own power contributed and responded to my involvement. Finally, I draw conclusions as to what my findings and reflection may contribute to the field of SDM as it is practiced in environmental governance.

### **Findings: Participant Relations**

Roles within workshop teams (coach, team coordinator, or team member) determine participants’ responsibilities and ability to influence the decision problem framing, structuring, analysis, or solution before, during, and after NCTC SDM workshops. Team coordinators develop their team’s initial problem statement when they submit a decision problem proposal, including a list of possible team members, to NCTC as their application to attend an upcoming workshop. NCTC selects teams based on their proposal, then matches team coordinators with a coaching team. Team coordinators then liaise between NCTC, workshop coaches, and team members. During the workshop, they participate as team members. After the workshop, they are responsible for submitting a white paper to NCTC presenting their final decision framework prototype and describing their team’s experience developing their framework at the workshop.

Workshop coaches lead team members through the experiential process of developing, then refining, a rapid prototype of their decision framework, simultaneously acting as lead facilitators, decision analysts, and teachers. When possible, coaches work in teams of two with

complimentary skills or expertise, e.g., in modelling and facilitation. Before the workshop, coaches provide guidance to coordinators regarding the types of team members to invite: the decision maker(s) (or their representative(s)), subject matter or local context experts, and stakeholders, broadly defined. NCTC recommends group size (less than ten people excluding the coaching team), but coordinators initiate and organize their team's participation (i.e., coordinators control the invitee list). In team working sessions, coaches set the pace of progression; moderating participant contributions; choosing where dig in, where to push on, and where to circle back to later. Because coaches have prior experience guiding teams work through the SDM process (PrOACT), they can identify potential impediments to the team's success in advance, and they come to the workshop with a plan informed by pre-workshop calls with the team coordinator(s) and members.

Coaches are recruited for workshops through the USFWS-hosted NCTC listserv, or they are identified by team coordinators with whom they have a pre-existing working relationship. In some cases, coaches are past workshop observers. After attending a workshop as an observer, as I did in 2015, NCTC welcomes you back in apprentice and co-coaching roles at future workshops, which is how I was able to co-coach at the workshop in 2018. Occasionally, coaches are enlisted through open calls, and sometimes coaches recruit teams with whom they are already working and together they develop their team's workshop decision problem proposal. SDM workshops are also organized and facilitated at the state level by faculty and graduate students from Coop Units who serve as coaches for state cooperators (e.g., state wildlife agencies) and their partners, independent of NCTC.

SDM practitioners who participate as coaches or team coordinators at NCTC SDM workshops, engage in ecological research and governance through multiple roles. Many work for

federal or academic research institutions, predominantly the USFWS, USGS, and universities. Practitioners' professional identities include researchers, facilitators, decision analysts, and scholars. All of which are socially situated positions; thus, practitioners are embedded within pre-existing power relations. In some contexts, structural conditions privilege their contributions while in others they create constraints that moderate their capacity to act on their own behalf or to influence others.

Considered by workshop participants to be essential to helping team members work through the PrOACT process, coaches derive power from ideational sources. They possess knowledge and legitimacy from prior expertise and prior experience facilitating collaborative applications of SDM, as well as from their professional positions in government or academic institutions as scientists or statisticians.

Individuals who decide to use the SDM process (e.g., the team coordinator who submits a proposal for their team to attend the workshop) or how the process will unfold (e.g., NCTC, coaches) who design or organize, and lead workshop activities possess structural power that allows for active or implicit inclusion or exclusion of actors. Through their influence over team composition, they set bounds on the range of outcomes that may result from the week-long workshop. Team coordinators seize the structural power associated with a leadership position within the team when they submit their problem proposal to NCTC. With this move, they acquire the authority to provide the initial framing of the team's decision problem, and they are empowered to choose team members.

Structural power also manifests among the SDM cases I observed through elite-level relationships that provide access and entitlements. Team members often have pre-existing professional relations (e.g., cooperative agreements between agencies at state or federal levels, or

research collaborations between agencies and academic scientists). Once engaged in the network of SDM practitioners (e.g., after participating as a workshop), additional opportunities arise to acquire additional knowledge and legitimacy, and to build and use structural power.

The benefits of access and entitlements provided by structural conditions to some, marginalize others by limiting their opportunities to bring forward issues or solutions (Brisbois & de Loë, 2016; Flyvbjerg, 1998). In the SDM cases I observed, members of the public or representatives of socio-economic interests were rarely represented on collaborative SDM teams. Because participation begets opportunities to build relationships, learn new skills, and get involved in other professional spaces – all of which contribute to a participant’s power in conservation contexts, limited stakeholder exposure/access to SDM processes may perpetuate existing power asymmetries.

Capacity imbalances in financial, social, institutional, or technical resources (i.e., material sources of instrumental power) shape workshop participation as well. Coaches volunteer their time and expertise in exchange for travel cost reimbursement and free accommodations, but workshop participants (observers and team members) pay a course fee that includes on-site accommodations, and they are responsible for their own travel expenses to and from the workshop. Most workshop attendees work for Department of the Interior (DOI) agencies, which provide support for their attendance. My attendance at the 2015 workshop at NCTC would not have been possible without funding from the GA Coop Unit for travel costs and course fees, and permission from my advisor and my teaching assistantship supervisor to be away from campus and my responsibilities on campus for a full week. My teaching assistantship supervisor was supportive; the focus and title of the course we were teaching was Conservation Decision Making.

Discursive power, legitimacy, and authority are interrelated due to the role of accepted truths and knowledge (Fritz & Binder, 2020; Partzsch & Fuchs, 2012). Practitioners are the primary contributors to SDM literature and have been for decades. Outside of workshops, they contribute to the discourse through their scholarship in the form of publications in peer-reviewed literature, writing books, developing training manuals, authoring white papers or grey literature, and giving conference presentations. As noted earlier, many practitioners are employed as academic or agency scientists. Academia incentivizes researchers' contributions to their field of expertise by rewarding individuals who publish in scientific journals with promotions or tenure. Within more rigid organizations, however, procedural and administrative hurdles can limit practitioners' discursive influence. This is more likely in agency settings than academic. For example, policies of some agencies restrict the language and tone of how a scientific finding may be communicated, which potentially shapes discourse about putting science into action.

### **Reflection: My Multiple and Mobile Roles.**

While pursuing my doctorate, I participated in SDM in multiple capacities, all of which were a product and perpetuator of relational power disparities. Across the contexts of my engagement, my positionality (Adler & Adler, 1994, pp. 377 – 392) may be generally described as a novice SDM practitioner who works among governance spaces as a quantitative ecologist, wildlife population modeler, decision analyst, teacher, participant observer, facilitator, and coach.

As a graduate student in the Georgia Coop Unit in Warnell I was afforded legitimacy, knowledge, instrumental resources for professional development, and elite relationships. Being vetted and selected by my dissertation advisor for the graduate assistantship working on the alligator decision-support project mentioned earlier provided me with sufficient legitimacy to put

me at the table next to my advisor when we met with the professionals with authority and knowledge of alligator harvest management practices and program history.

At the NCTC workshops I attended, I met professionals who earned their graduate degree through the GA Coop Unit or previously worked with my advisor, and some of the USGS researchers serving as team coaches were familiar to me because we previously interacted in the context of the alligator harvest management workshops that my advisor and I organized for the harvest management decision-support project. It was a pleasant surprise to see some familiar faces at my first workshop in 2015 because I did not know of anyone else before my arrival. I saw some of the same individuals again at the 2018 workshop, as well as at population modelling workshops at the USFWS Patuxent Wildlife Research Center in Laurel, MD, in 2013 and 2016. These connections extended my legitimacy beyond of the university, among other conservation professionals associated with SDM, including USGS and USFWS professionals at NCTC, and NCTC.

As a result of the training (knowledge) and legitimacy I gained from my assistantship work and my experience at NCTC, I was given opportunities to teach SDM to undergraduate students formally through the conservation decision making course offered in Warnell that I previously mentioned, and I organized seminars and training workshops for my peers as well as members of the public with whom I interacted during a Public Service and Outreach graduate assistantship with the J. W. Fanning Institute of Leadership Development at UGA. Along with my research and scholarship, my instructional roles are a product of and contributor to discursive power.

In the case of the alligator project, my contributions were primarily as an analyst. I focused on developing decision-support tools to improve scientific understanding of population

dynamics and directly applying that understanding in evaluating decision alternatives. My advisor developed the project proposal that secured funding for the work, primarily travel costs for in-person meetings with collaborators and expenses associated with hosting inter-agency workshops. The project was inspired by my advisor's early career work, thirty years ago, with the Florida Fish and Wildlife Conservation Commission.

Despite a relative abundance of alligator population data available, actionable science about species biology had been limited over those years. Available technology (computers) lacked the capacity to handle large data sets and complex statistical models, which prevented alligator population managers from using existing data in decision making. With advances in technology and statistical tools derived from Bayesian statistics over the last three decades, and my advisor's work in early applications of SDM and AM, it seemed like the right time to revisit the issue with new tools.

The decision to develop a SDM framework for alligator harvest programs and to use an integrated population model to improve population parameter estimates and forecast management outcomes under different policy options had been made when I joined the project. My advisor had also decided what type of expertise was needed to conduct the project, from where credible information could be acquired, and the different types of information needed for analyses. This led to my advisor hiring me for the work and is why we reached out to the alligator harvest program managers for their population data. Since then, most of the decisions, e.g., how uncertainty is acknowledged and addressed in both analyses and communications regarding the analyses, have been my responsibility, but they are approved by my advisor.

With guidance from my advisor and informed by what we learned from alligator harvest managers about their decision-support needs, I developed an alligator population model and

conducted a pilot analysis to demonstrate how it may be used to identify an optimal harvest policy. Many judgements calls were required throughout the research process, including my choice of methods, inputs used in analyses, and determination of which assumptions were reasonable, all of which influences the results of my analyses.

The results of my quantitative analyses depend on the confluence of me (my knowledge and skills – analytical, interpersonal, and tactical) and my access to capable technology (e.g., computer processing power). Along with an understanding of statistical theory and methods, the statistical models I use require programming expertise. My analyses required proficiency manipulating data, developing models, and analyzing results in the program R, as well as having a working knowledge of Linux systems and coding in the programming language bash to run analyses remotely on multicore computers that have sufficient memory and processing power to complete computationally intensive jobs efficiently.

### **Illuminated through the Power Lens**

Relational power is a useful analytical lens for making visible and connecting sometimes opaque factors underlying natural resource management applications of SDM in the United States. It reveals the influence of structural conditions on individual and institutional agency. Government researchers and academic researchers (including principal investigators and their graduate students, such as myself) fill different roles among teams, primarily brokering roles as coaches and decision analysts. In collaboration with NCTC, they design, facilitate, and report on collaborative SDM applications.

Identifying these connections helps us understand how actors, their socially structured relations, and power dynamics created through their interactions co-construct SDM practice and professional discourse. Power determines degree of inclusivity and transparency of SDM

processes. Good governance is not guaranteed by the process itself but by the practitioners and participants engaged therein. Whether the opacity of power in transparent accounts of SDM is an artifact of practitioners' blind spots or an intentional omission is important to our understanding of how SDM collaborations emerge, succeed, or fail, and are reported, and where adjustments may overcome shortcomings. Different issues are at play, requiring different mitigation methods.

If SDM can do/does all that is claimed, why does the decision-implementation gap exist? Ostensibly, if analysis of a structured decision identifies an optimal choice, the decision problem is no longer a problem. Yet, recommendations produced through the SDM PrOACT process for wildlife management issues may have little or no impact on management actions or policies. Structural conditions around coaches and team coordinators, specifically pre-existing relationships among individuals and their institutions (e.g., long-term partnerships between USGS and USFWS, or among Coop Units and their in-state cooperators), may contribute to discrepancy between the "decision maker" who participates in developing the framework versus the legal or financial authority who determines implementation, as demonstrated in the alligator harvest management decision-support project.

Although scientists occupy an influential position in SDM applications when serving as a coach/facilitator, science is not necessarily more influential. Developing technical solutions to reduce scientific uncertainty and improve decision defensibility may improve how available data are used to provide decision guidance, but whether that guidance is followed depends on several factors. Among them is whether the real decision maker participated in decision structuring and whether they fully articulated their fundamental objectives. In the alligator project, for example, the real decision maker in terms of who has the final say, veto power, regarding annual harvest policies was not the person with whom we engaged. It is common practice in my experience to

have a representative of a decision maker participate in the collaborative PrOACT process. Engaging the person(s) with ultimate authority, instead of their proxy with whom we already interact, may help ensure we're solving the right problem. When a framework is populated by a limited sample of voices or stand-ins participating in place of unengaged decision makers, it risks throwing itself into the decision-implementation gap described in Wright et al. (2020).

### **Reflexivity through Autoethnography**

The situatedness of conservation scientists within political and social processes necessitates research methods with complementary socio-political structures and processes, and opportunities for iterative reflection and revision, which fall beyond the scope of traditional disciplinary training methods (van Kerkhoff, 2014). For SDM practitioners, and conservation researchers in general, I recommend autoethnography as method despite coming to it myself by default.

As insights accrued experientially during my engagement with SDM practitioners and participants, I made note of them. I did so without a formal protocol because, until recently, I had no intention of sharing them. Over time, I started noticing the patterns presented in this chapter as they emerged, revealing new questions about practice and research interests, such as how relations between individual agency and structural conditions affect the SDM process and implementation of its outcomes. Note, agency here refers to an individual person's capacity to act on their own behalf; not government institution such as a state department of natural resources. Without the foresight to get human subjects research approval to study relational power dynamics among individuals in my professional network, opportunities for me to investigate further or share my "insider knowledge" were limited.

Autoethnography provided a means to share cultural knowledge assimilated during the process of professional development without requiring IRB approval for human subjects research. It gives voice to assimilated knowledge and provides a means to share this history with the next generation of applied research scientists, SDM practitioners, and integrative researchers. Autoethnography provides space for reflexivity as well as sharing tradecraft with colleagues.

### **Conclusion**

Decision structuring and analysis approaches are subject to, and serve to perpetuate, historic power asymmetries within the field of conservation. Power structures are unchallenged by current SDM practice. The flexible framework works with existing actors and is not a threat to top-down control. Sharing power or restructuring decision authority/responsibility is not obligatory. Adopting a SDM approach to resource management challenges can enable managers to be more inclusive of different stakeholder voices while allowing state actors to retain their authority to shape the process and its outcomes in a way that perpetuates existing top-down models of natural resource management.

SDM may be grouped with other well-intentioned efforts to engage in interdisciplinarity, but which ultimately privileges one epistemological perspective over others in defining questions and guiding research (Turkle & Papert, 1990). SDM practice, the actors and institutions promoting the approach are interdependent, mutually contributing to the structural, instrumental, and discursive power dimensions. Asymmetry in expressions of power and control need to be acknowledged and questioned to potentiate the transformative capacity of transdisciplinary processes (Lawrence, 2015). Additionally, scientists may wish to play multiple roles to maximize efficiency of a multi-objective decision process (Wright et al., 2020). Blurring the line between scientific roles (e.g., subject matter experts, analysts) and leadership positions (e.g.,

coordinator, facilitator) in application can undermine practitioner legitimacy to stakeholders and decision makers by eroding their status as an impartial honest broker (Rantala et al., 2017; Wright et al., 2020).

What we know about practice from the published literature raises questions current practitioners may be ill-suited to answer. This undermines our understanding of how decision analysis contributes to policy changes or actions, or other measures of public value. Not only may the environment be changed by environmental projects; interdisciplinary teams can foster mutual learning (Goggin et al. 2019). Lessons learned in practice but not documented and disseminated among descriptions of real-world applications may be effectively captured by a broader coalition of researchers and practitioners. Bridging the decision-implementation gap will likely require insights gleaned by researchers trained to apply and develop theory pertaining to human behavior, the workings of power, organizational science, and collaborative resource governance. Ignoring how power is involved misrepresents influential elements of case studies. It also contradicts common claims that SDM frameworks improve transparency, which may undermine reproducibility as well as the credibility of published accounts.

## CHAPTER 6

### **Synthesis, Reflection, and Conclusion**

#### **Synthesis**

Federal and state resource management agencies in the US occupy privileged positions in wildlife conservation and management contexts. Their decisions, and the processes leading to them, affect members of the public in non-random ways. The overarching aim of my dissertation was to understand decision support solutions developed to link available data and expertise to agency policy deliberations so decision makers may better understand their options. Each “solution” – a population model (Chapter 3), harvest policy function (Chapter 4), and decision-making process (Chapter 5) – is useful independent from the others in a specific context – wildlife research, harvest management, or collaborative decision making, respectively. Together, they highlight how conservation researchers are involved in wildlife management at multiple scales of governance, and how in the framing of problems, different perspectives highlight and obscure different parts of the management context. In my final chapter, here, I review what can be learnt from each of the preceding chapters in terms of their disciplinary contribution. I discuss how complexity and context – principles of integrative research – manifested in relation to the decision support solutions I examined, and summarized what is lost and gained by each approach to knowledge generation. Lastly, I reflect on the integrative research process, the value-added by pluralism and reflexivity, and I acknowledge the boundaries of my results.

In my first two empirical chapters (Chapters 3 and 4), I use a simulated alligator population to evaluate analytical tools available to translate existing population data into scientific knowledge and decision guidance, respectively. In Chapter 3, I developed an integrated population model (IPM) for alligators to estimate population parameters needed to understand

responses to harvest. To study the IPM's behavior before fitting it to real data, I used simulation to conduct multiple trials, each one fitting the alligator IPM to a replicate set of data, which were created to resemble alligator mark-recapture-recovery data, harvest data, nesting data, and count survey data collected from Orange Lake, FL, during the FFWCC's experimental harvest (1981 – 1990). The results from the first ten trials indicate the framework has the potential to overcome the shortcomings of past alligator harvest models. With an IPM framework, past investments in alligator research and monitoring reified in agency data may yield new returns in the form of more accurate and precise population parameter estimates. Reliable parameter estimates are key to resolving scientific questions about the alligator populations and the inter-relationships between alligator ecology, population biology, and management.

In Chapter 4, I demonstrated a technical solution to a long-standing challenge in alligator harvest management: setting annual hunt quotas to optimize management objectives given observed population state and scientific understanding of population responses to harvest. I used a genetic algorithm to identify a harvest policy for setting annual harvest quotas using annual monitoring data. The approach integrates existing data streams and management objectives through a harvest policy function and, in the process, enables science to inform management in a consistent and justifiable manner. The genetic algorithm optimizer uses forward simulation to predict population outcomes under alternative policy options, then makes comparisons among policy alternatives in terms of how well they achieve management objectives.

In their current state, both the alligator IPM (Chapter 3) and harvest policy optimization (Chapter 4) are theoretical demonstrations of analytical tools. They are incomplete in the sense that in Chapter 3, model verification trials need to run longer (i.e., for additional iterations) to allow the model to reach convergence on the posterior distribution for all of the model

unknowns, including latent states (e.g., size class abundances) and discrepancy measures that were not monitored in the preliminary analysis presented in Chapter 3. I consider Chapter 4 to be incomplete because candidate harvest policy solution fitness scores are unstable. The signal from the optimal policy, in the current formulation of the optimization routine, may be due to chance. Alternatively, the effect from candidate solutions maybe swamped by “noise” generated by stochasticity built into the management system simulation model. It is also possible there are many equally good solutions for the harvest policy and different considerations (objectives) may be needed to further differentiate candidates. Additional testing is required. Both chapters are demonstrations because they use data simulated from a hypothetical latent population, itself simulated. They are theoretical because the underlying population and observation processes specified in the simulation models were developed according to published alligator research results and data, most from the alligator population at Orange Lake, FL. The results are promising; they illuminate a new frontier for alligator research and management with the potential to transform work in both areas. In their current form, however, their practical value is limited to adapting the simulation and analysis code files I created (Appendices C, D, and E) to build intuition regarding how the IPM and GA perform under different constraints and conditions.

In my third empirical chapter, Chapter 5, I present an autoethnography of my experience engaging in structured decision-making applications for conservation. I used the realist theory of (relational) power to reveal the enduring structural preconditions shaping participants’ interactions in ways that are rarely unacknowledged but consequential. Social structures, such as team member roles, positions within organizational hierarchies, and areas of expertise shape agent (participant) interactions and power relations among conservation professionals in multiple

ways. Notably, we see how multiple and mobile relationships among SDM practitioners from federal agencies and research institutions use existing structural conditions to exercise and accumulate discursive power.

### **Complexity Addressed, Complexity Neglected**

Each of my empirical chapters approached complexity in conservation and management decisions in a distinct way, each attending to some characteristics of CASs while ignoring others. Chapters 3 and 4 acknowledge sources of uncertainty inherent to population research and management efforts. In Chapter 3, different types of population data collected at multiple scales (individual and population levels) are simulated under conditions of imperfect detection then integrated within a coherent modelling framework that allows for sharing of information among hierarchically structured parameters, describing random effects and errors in variables (Clark et al., 2005). The framework incorporates stochasticity through probabilistic, rather than deterministic, population and observation processes. Simulating replicate data sets allows for capturing a range of outcomes that may arise under the model due to stochasticity alone.

The state-space formulation in the estimation model accounts for our inability to observe or describe nature as it really is by differentiating between the true latent population about which we want to make inferences and our partial observations of it captured in data. Multiple models are required to capture alternative hypotheses regarding the functional form and interrelationships among latent population processes and observation processes. Without competing models, structural uncertainty is ignored for the time being and the estimation model is used to resolve parametric uncertainty. In the estimation model, environmental drivers of population processes and density-dependent processes are not described. Importantly, the model verification presented in Chapter 3 examined whether the estimation model is performing as

expected, but it provides no information regarding the model's validity. That is, the analysis presented in Chapter 3 says nothing of how well the model describes reality.

In Chapter 4, the simulated management system recognizes partial observability of alligator monitoring data available to managers setting annual harvest quotas as well as partial controllability of harvest implementation. Stochasticity was incorporated into the management system models in Chapter 4 in the same way as was done in Chapter 3, i.e., through probabilistic processes, then fifty replicate time series, which presumably capture the range of stochastic realizations of the population that may be possible under each candidate policy option in the GA population, were used to compute the fitness score for each policy.

The genetic algorithm employed in Chapter 4 is oriented to solve a problem, but it can only solve the problem as perceived (Becker et al., 2005). Underlying the optimization procedure is the assumption that population process relationships described in the simulation model are correct and static with respect to time (i.e., structural relationships and parameters are constant). Similarly, it assumes objectives do not change. Given the dynamic nature of CASs, these assumptions are likely to be violated *in situ*. Nonetheless, heuristics (e.g., genetic algorithms) and probabilistic methods of simulation, though unable to identify stable and robust solutions when the underlying system changes, still may improve our understanding of the solution space (Tolk, 2022).

The analysis of relational power in Chapter 5 demonstrates interrelationships between SDM practitioners, practice, and scholarship that exhibit nonlinear dynamics, particularly, positive feedbacks among structural and discursive power dimensions that result in clustering of knowledge and legitimacy in wildlife management networks. Interdependencies such as those that exist between USFWS, USGS, and Coop Units are rarely acknowledged in published

examples of SDM applications, but they may confound system observations and inferences based on them regarding participant experiences or process outcomes.

### **Context Recognized, Context Ignored**

As noted in Chapter 3, due to regional differences in alligator populations, an alligator IPM parameterized for one population may not be generalizable to others. Instead, IPMs for real alligator populations may need to be adapted to their context. This much has been recognized since the FFWCC conducted its experimental harvest in the 1980s. It remains to be seen what an alligator IPM for (real) OL alligators will look like in terms of its structural elements (population states and demographic rates) and their inter-relationships (e.g., through DD processes). In some places interrelationships between harvested alligators and segments of the population targeted by multiple management programs (e.g., separate private lands harvest programs) may need to be incorporated.

Optimization is a desirable, but unnecessary, component of decision making. For recurrent decisions, adaptive management acknowledges biological uncertainty about system behavior (structural uncertainty) and uses a strategy to adjust management decisions considering what is learned at each decision opportunity. In some contexts, this may be a better option for setting harvest policies. Assuming agencies have a common interest in using optimization to set harvest quotas, not all agencies have the same capacity to do so. Population modelling and optimization require training in statistical theory and computer coding, as well as (computing) technology.

Coop Units and external partners may be able to help, but it creates a dependency on specialized experts. Partnerships with Coop Units are common means for enhancing science and technical needs of agencies, but when projects are conducted by graduate students (who are still

learning, have different priorities and timelines), the services and deliverables produced may not suit managers' needs. For example, Chapters 3 and 4 remain theoretical at this point; not helpful until used with real data. I will discuss this further at the end of this chapter when I reflect on my role within my system of study.

Another important contextual caveat associated with Chapter 4 that is worth noting is that monitoring and policy cycles for alligator harvest programs are not aligned. In the simulated alligator harvest management system that I used in the optimization routine, annual population count data are generated at the end of the summer/beginning of fall as input for the harvest policy function. The policy function then outputs a quota and an inefficient harvest process (i.e., one subject to partial controllability that results in less alligators being taken than the quota allowed) determines the number of alligators harvested from the observed population (i.e., source of the counts). Even with a streamlined process that takes in monitoring data and returns a quota (i.e., monitoring data do not need to be analyzed first to produce a population size estimate before identifying a recommended quota), harvest quotas for alligator hunting season are established before summer monitoring surveys are conducted. Monitoring surveys occur in summer months when alligators are more visible. In the winter alligators are hard to find. Unfortunately, harvest regulations in many states are reviewed and adopted for many species at the same time when it fits into the legislative schedule of state governments (e.g., in Georgia it occurs during winter after the beginning of the calendar year). This means forces beyond the control of alligator managers prevent alignment of population monitoring and policy cycles, regardless the harvest policy that is adopted.

Focusing on technical problems and solutions without considering the context in which they will be applied risks wasting resources to develop products that are not viable. The incentive

for managers to change their decision-making process may be low. Despite its merits, adapting to a new approach to decision-making (particularly if it is for a singular management problem/program and not established as an agency norm) incurs costs.

The irreversible allocation of participants' time towards engaging in a SDM process is itself a decision (i.e., an allocation of resources to follow a course of action) that is influenced by context (Howard, 1968). Tradeoff decisions are required throughout the model development and implementation process, as well as in designing collaborative SDM frameworks, though formal analyses are rarely employed. Instead, these tradeoffs are made implicitly without providing opportunities for others to weigh in.

Managers face a tradeoff in deciding whether to adopt decision support tools created by applied scientists. In some cases, existing reactive approaches to management, which tend to be functionally simple but riskier, are performing adequately, achieving management objectives often, e.g., cranes (Gerber & Kendall, 2018) and public alligator harvest management in the species' eastern range. When the status quo has yet to fail them, the potential increase in expected performance of a more complicated but defensible decision process may not be worth the short-term investments required for its adoption (Gerber & Kendall, 2018).

### **Conclusion**

Advances in technology and statistical theory are providing new opportunities to study wildlife populations and their responses to conservation and management actions. I demonstrated methods available to improve the scientific basis of decision guidance and use of available data directly in evaluating management alternatives. I also reveal how the discursive and instrumental power of the tools, or theory behind them, relies on practitioners' structural conditions and social relations. Institutional structures limit the decision-making authority of agency researchers and

managers. In hierarchically structured agencies, SDM practitioners are limited to making recommendations with a more credible process, and while structured decision-making facilitates, stakeholder inclusion, empowerment, or transparency, these qualities are not inherent to the process. Whether and how researchers' contributions infiltrate management policies or catalyze a culture shift depends on more than the researcher's and their collaborators' buy-in. Decision recommendations generated by agency professionals, regardless of the quality of the process, can be vetoed by a superior within their organizational hierarchy who possesses greater authority.

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## **Appendix A**

### **Decision Support for Public Alligator Harvesting in Georgia, Florida, and South Carolina: Final Report to USGS Cooperative Research Units Program**

# **Decision Support for Public Alligator Harvesting in Georgia, Florida, and South Carolina**

## **Final Report to USGS Cooperative Research Units Program**

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## Decision Support for Public Alligator Harvesting in Georgia, Florida, and South Carolina

*Abstract:* The American alligator is a game species in most U.S. states within its range. Typically, harvest regulations are determined annually or biennially based on the statistical estimation of trends in counts of monitored populations. Although this quantitative approach leads to a harvest quota decision, it is not one that is based on alligator population dynamics, and so may be problematic in three aspects. First, the alligator's life history is like that of no other North American game species, with life stage dynamics that play out over decades. Thus, the use of statistical models to project past abundance patterns into the future may be a less robust means to predict response to harvest for this species than for typical game species with shorter life cycles. Second, key uncertainties that affect how harvest is conducted – for example, the degree of compensation in survival or productivity – cannot be explored and resolved without incorporating such mechanisms in a biological model. Third, a decision framework based on statistical modeling of trend is unable to directly inform any harvest management objective that explicitly recognizes population sustainability, whereas population persistence is a natural byproduct of a mechanistic-based population model. The main objective of this research was to start a decision structuring process for public alligator harvest in the eastern portion of the species' range (Alabama and eastward), developed on a mechanistic model framework. To this end, we developed collaborations with state wildlife agencies in the region; we conducted workshops with agency biologists and managers to elicit information about current processes, agency-specific objectives of management, and scientific uncertainties; and we built a biologically-structured dynamic population model that could serve as the predictive basis of a formal dynamic decision framework.

### Introduction

#### *Problem Background*

The public harvest of the American alligator (*Alligator mississippiensis*) across its range – currently permitted in the states of Texas, Arkansas, Louisiana, Mississippi, Alabama, Florida, Georgia, and South Carolina – is regulated by respective state wildlife agencies. Each agency operates under its own harvest goals and regulatory frameworks, and quotas are applied in different spatial contexts and to different population components (eggs, hatchlings, non-hatchlings).

However, there are some commonalities in how agencies approach harvest regulation of alligators, certainly in the eastern part of the range (Alabama and eastward). Here, all agencies rely on an annual measurement of the population to guide the choice of each season's regulatory action, all collect similar types of population and harvest data, and all conduct management across a region in which alligator population dynamics and response to harvest may be similar within broad physiographic divisions.

In these eastern states, selection of the harvest regulation is based on fitting a locally-smoothed trend line to monitoring data and analyzing the position of the current-year predicted mean relative to established decision triggers. The specific modeling approach and choice of decision triggers differ among agencies, but a statistically-based evaluation is the core of the decision framework.

The appeal of statistical model-fitting approaches for making harvest decisions is that incorporation of the trend line helps to stabilize large annual swings in the raw counts. Their use also mostly automates the regulations-setting process. However, the models describe only the observed phenomenon over time, not the underlying biological mechanisms. They do not describe how populations respond to harvest and population density through their effects on survival and recruitment. A model that includes

these mechanisms may be able to predict a real population response induced by harvest, whereas a statistical model can only interpret the observed response in the context of the preceding trend and thus may discount it as unexplained noise. Another challenge posed by the use of statistical models is that the level of smoothing chosen is arbitrary; even if model selection is data-guided, the choice of parameterization for a given survey area may change year to year in a way that is not biologically explainable. Because mechanistic models are built on biological processes, their predictions tend to be robust in circumstances that are outside of historical experience (Williams et al. 2002:30).

Alternatively, dynamic control models predict population density or other resource outcomes based on currently-observed population states, relevant environmental conditions, and the proposed management action (Williams 1989). Mechanisms such as survival, productivity, and their responses to management actions are embedded within these models. A distinct advantage of working with such models is that an optimal management action for an identified objective can be chosen with respect to both (1) current conditions and (2) expected response to the action and future behavior of the system. First, the choice of an optimal action is conditioned only on current population status and (perhaps) current environmental conditions: the past trend of population is not considered. This approach yields decision thresholds or “trigger points” that indicate a specific action to take when certain conditions are reached. Second, the selection of an optimal action accounts for the expected response to the action and the expected long-term effect on the resource under future actions. Because the future status of the resource is explicitly accounted for in decision making, the decision policies delivered by this approach are by definition sustainable.

Another advantage of using dynamic control models is evident when biological uncertainties make it difficult to choose among alternative management options (Nichols et al. 1995). Competing theories about the biological response of the population to harvest may imply that different strategies are best for a given management goal. Such uncertainties can be represented as a set of competing models, with each model proposing a different response to a given action. Because dynamic control models employ mechanistic relationships, constructing a set of models around biological uncertainties is more straightforward in this context than in the statistical model-fitting context. Decision making under a set of competing models, with the opportunity to evaluate the performance of those models through the collection of monitoring data, forms the basis for a formally adaptive approach to harvest management.

### *Objectives*

The main objective of this research was to start a decision structuring process for public alligator harvest in the eastern portion of the species’ range. We set out to accomplish this by:

- Developing collaborations with state wildlife agencies in the region;
- Conducting workshops with agency biologists and managers to elicit information about current processes, agency-specific objectives of management, and scientific uncertainties; and
- Building a biologically-structured dynamic population model that could serve as the predictive basis of a formal dynamic decision framework.

### **Summary of Activities**

#### *State Agency Collaborations*

The focus of our investigation was the states in the eastern portion of the alligator’s range that conduct programs of public alligator harvest: Alabama, Florida, Georgia, and South Carolina. Florida has the

longest period of sustained alligator research and has permitted harvest in some form since the 1980s. Florida was first in this region to establish quantitative guidelines for harvest based on recurrent population surveys. In succession, the states of Georgia, South Carolina, and Alabama established harvest programs modeled to some degree on the methods used in Florida. While North Carolina currently does not have a public alligator harvest program, the North Carolina Wildlife Resources Commission (NCWRC) is considering the value and biological feasibility of a harvest program.

In a series of meetings held September-November 2013, we conducted “listening sessions” with representatives of each agency: Alabama Department of Conservation and Natural Resources (ALDCNR), Florida Fish and Wildlife Conservation Commission (FLFWC), Georgia Department of Natural Resources Wildlife Resources Division (GADNR), and South Carolina Department of Natural Resources (SCDNR). Following a presentation on the goals of our project and an introduction to concepts of structured decision making (SDM), we conducted a wide-ranging interview with the attendees. The interview was facilitated by distributing a questionnaire (Appendix A) prior to the meeting in which agency respondents were asked open-ended questions about the structure of their management program, the objectives of the program, management alternatives that they used, the method of choosing an alternative when setting regulations, the nature of their monitoring program, critical uncertainties that make decision making challenging, and areas of dissatisfaction or concern with their program.

We compiled these responses in the form of a table that portrays comparatively how each agency approaches the different components of harvest management (Appendix C). The comparative analysis is useful as a starting point for considering how public harvest management in each state can be approached as a formal decision problem. Similarity among states in some attribute suggests some degree of universality with respect to that attribute. Substantive differences in other attributes point to decision components that would be structured separately among states. The table was of great interest to the state collaborators, as they had never seen a side-by-side comparison of their own agency’s program with others in the region.

We are preparing a manuscript for publication in the *Wildlife Society Bulletin* that assesses the diversity of management policies and practices among agencies. Program elements are evaluated in the context of the principles of SDM, with an exploration of how additional value may be brought to the program by further development of the elements under an SDM framework.

To assist us in the development of a decision model, agencies provided us access to harvest and population monitoring data. Additionally, some data from research studies were shared with us.

#### *SDM Workshops*

We conducted a 3-day workshop in December 2013 (GADNR Coastal Resources Division, Brunswick GA) and a 1.5-day workshop in December 2014 (J.W. Jones Ecological Research Center at Ichauway, Newton GA) to further discuss agency approaches to harvest management and to consider how a formal dynamic decision framework built on a population model foundation could be structured (Appendix B). Agency biologists and managers from all states in the focal region, including North Carolina, attended both workshops. Additional outside experts from USGS and University of Georgia attended one workshop or the other, offering additional insight and helping to facilitate small group exercises.

Workshop 1 (2013). Topics treated at this workshop included problem definition and management contexts, identification of management objectives, identification of management alternatives, model structure, and monitoring strategies.

- **Management Context:** Participants first discussed the management context in their state, describing the spatial distribution (e.g., population units vs. zones) and temporal recurrence of decision making and how the quota-based regulatory system works.
- **Fundamental Objectives:** Next, participants worked in small groups (keeping state representation balanced across groups) to identify fundamental objectives of management. In whole-group discussion, participants identified eight fundamental objectives that were important to one or more of the states: (1) assure population sustainability (conservation of the resource over space and time), (2) increase opportunity for consumptive use, (3) increase opportunity for non-consumptive use, (4) increase hunter satisfaction, (5) decrease human conflicts, (6) increase cost-effectiveness, (7) increase opportunity for commercial interests, and (8) respect process objectives and constraints. Breaking back out into state groups, participants provided relative importance scores to each of the fundamental objectives (Table 1). The exercise revealed the relative value each state attached to each objective, as well as consistency or diversity among states in valuing objectives. Over all states, the population sustainability objective was the most highly valued, and it exceeded the second-most highly valued objective by at least 1.5 times. Discussion about objectives concluded with the entire group identifying specific metrics or indirect indices that could be used to measure satisfaction of each objective.
- **Management Alternatives:** In state-by-state presentations, participants provided a summary of the regulatory structure and options available for selection.
- **Model Structure:** Participants worked in small groups (keeping state representation balanced across groups) to consider alligator population demographic processes (survival, reproduction, movement) and the controllable and non-controllable factors that influence them. The groups were challenged to present these relationships in an influence diagram. Each group in turn presented a summary of their discussions to the entire group.
- **Monitoring Strategies:** In state-by-state discussions, participants provided a summary of their monitoring program and protocols. An entire group discussion followed, identifying strengths and challenges of these programs.
- **Wrap-up:** The workshop concluded with a review of previous discussions, followed by a general discussion of data sharing, how the group collaborates, and next steps to take.

Table 1. Relative importance scores (normalized to 100 total points) assigned by state representatives to each fundamental objective of harvest management.

Fundamental Objective	Alabama	Florida	Georgia	South Carolina	North Carolina <sup>1</sup>
Population sustainability	30	30	55	40	60
Consumptive use	10	15	15	10	5
Non-consumptive use	8	5	5	5	5
Hunter satisfaction	15	15	10	10	0
Human conflicts	10	5	10	15	20
Cost-effectiveness	15	20	3	5	10
Commercial interests	5	5	2	5	0
Process objectives	7	5	0	10	0

<sup>1</sup>North Carolina has no harvest program but their representatives participated in the exercise.

Workshop 2 (2014). This workshop continued the modelling discussion started at the 2013 workshop. Based on notes from the 2013 workshop, and prior to the 2014 workshop, we constructed a generic influence diagram to identify factors affecting survival, productivity, and harvest availability. The workshop then proceeded through cycles of small group work and whole-group discussion and consensus. In the first exercise, three teams were formed (keeping state representation balanced across groups), and they were given large posters of the generic model to mark up and critique. Their charge was to evaluate the completeness of the generic model and determine whether important factors or relationships were overlooked. In whole-group discussion, the comments were compiled and displayed in a revised version of the model. In the second exercise, the same teams were given posters of the revised model, and they were asked to (1) determine which components could be measured as part of a monitoring strategy and (2) which components are likely to have greatest influence in most situations, i.e., which are too big to ignore. Teams reached consensus on these points in the subsequent whole-group discussion. In the third exercise, the teams were asked to provide some detail (directionality, form, dependencies) for each of the important drivers (habitat, hydrology, population density, harvest) on survival, productivity, and harvest availability. The fourth exercise focused on identification of critical uncertainties. Individually, participants were asked to write down a small number of conditions that make outcomes of management hard to predict. Regrouping into their teams, the participants were asked to compare notes and achieve consensus about those forms of uncertainty that most affect the ability to make a good decision. The fifth exercise focused on important gradients and strata that may influence alligator population dynamics and response to harvest. In a whole-group discussion, participants came to consensus on three key gradients (mean temperature, fresh water availability, and nutrient level) that vary across the region and are thought to influence population dynamics. In their teams, participants were asked to provide details (directionality, form, dependencies) on how these gradients are believed to affect survival, productivity, and harvest availability.

### *Model Development and Simulation*

Any mechanistic model that could inform a dynamic decision process for harvest management would be constructed around a representation of the life cycle of the alligator. However, life cycle models of alligators are rare. Nichols et al. (1976) built a sex and age-structured model parameterized from vital rates measured in Louisiana, and they simulated it on a monthly time step to investigate different levels of fixed harvest rate. Woodward (1996; Appendix B) reported a sex and age-structured model informed by vital rates measured through studies conducted on Orange Lake, Florida. The model was simulated in monthly time steps and was used to explore different strategies of fixed harvests of eggs and harvests of adults. Dunham et al. (2014) created size-stage transition models for alligators in the northern and southern portions of the range, parameterizing the models using published vital rates from corresponding parts of the range. Harvest was not investigated in their models; however, they simulated their models in annual time steps and explored potential scenarios of climate change through hypothesized influence of temperature and precipitation on vital rates.

These models all proposed a state and transition structure, and they were parameterized with vital rate information (survival, growth, reproduction) obtained from other studies. The models either were not tested against field data (Dunham et al. 2014), were found to predict satisfactorily in limited testing (Nichols et al. 1976), or were found to be unreliable in many tested scenarios (Woodward 1996). For process models parameterized from vital rate information, it is not uncommon to find that model predictions fail to match observed abundance data (U.S. Fish and Wildlife Service 2002) or to project reasonable patterns of growth (Cummings et al. 2017).

One potential solution is to consider vital rate information and observed abundance data (e.g., counts from a monitoring program) in a common modeling framework in which parameters informed by both sources of data are jointly estimated. In an integrated population model (IPM), the unobserved population is the state of interest for estimation, and monitoring data and vital rate data together provide information about overall abundance and change in abundance over time (Schaub and Abadi 2011). Each data stream is subject to sources of error; however, the inclusion of both in a single model with biological structure serves to reduce prediction error overall, compared to modeling the data streams individually.

The chief goal of our work is to build one or more integrated population models to be optimized to yield best harvest actions under a stated objective function. Steps toward that goal are:

- (1) identify the stage structure and time steps to be represented in a model;
- (2) construct a simulation model based on that structure, using literature-derived vital rate estimates as preliminary model parameters;
- (3) use the model to simulate a collection of data that could conceivably arise as part of a comprehensive population study – such a collection would include data on productivity (numbers of nests and clutch sizes), survival (mark-recapture of a sample of animals), abundance (night-light monitoring data), and harvest;
- (4) analyze the simulated data to parameterize an IPM and confirm that the preliminary model parameters are contained within the confidence bounds of the estimates of those parameters;
- (5) fit the IPM to field-collected data obtained from actual population studies; and
- (6) conduct model assessment to confirm that the model produces reasonable behavior and adequately predicts data not used to fit the model.

In this report, we describe results of steps 1 and 2. Steps 3-6 and model optimization will be performed in a later stage of Ms. Crawford's PhD work.

Using demographic data obtained on Orange Lake, Florida, we modeled a closed (to immigration and emigration), sex-structured population of alligators through successive size class stages in annual time steps (Figure 1). The model tracked size (total length; TL) of individual animals as they survived and grew through five successive stages: hatchling (TL <30 cm), juvenile (30 – <122 cm), subadult (122 – <183 cm), adult (183 – <274 cm), and bull ( $\geq 274$  cm). We fixed the transience time of the hatchling stage at one year, reflecting the first year of an alligator's life where it remains near its natal site and its nest mates. All other size stages had indeterminate transience times, where a size growth model determined the probability that a surviving individual graduated to the next larger stage. The juvenile stage reflected the growth period in which young alligators disperse and grow to harvestable size. The subadult stage represented the period in which alligators approached reproductive size and became vulnerable to harvest. The adult stage portrayed the size at which alligators may become reproductively active. The bull stage reflected a size threshold – reached almost exclusively by male alligators – that demarked a "trophy" harvest size class.

The anniversary date of the model was September 1, a date that follows completion of hatching but precedes the hunting season; thus, the model reflected a post-breeding census. The year was divided into six seasonal periods to facilitate the modeling of season-specific processes of harvest, survival, reproduction, and growth.

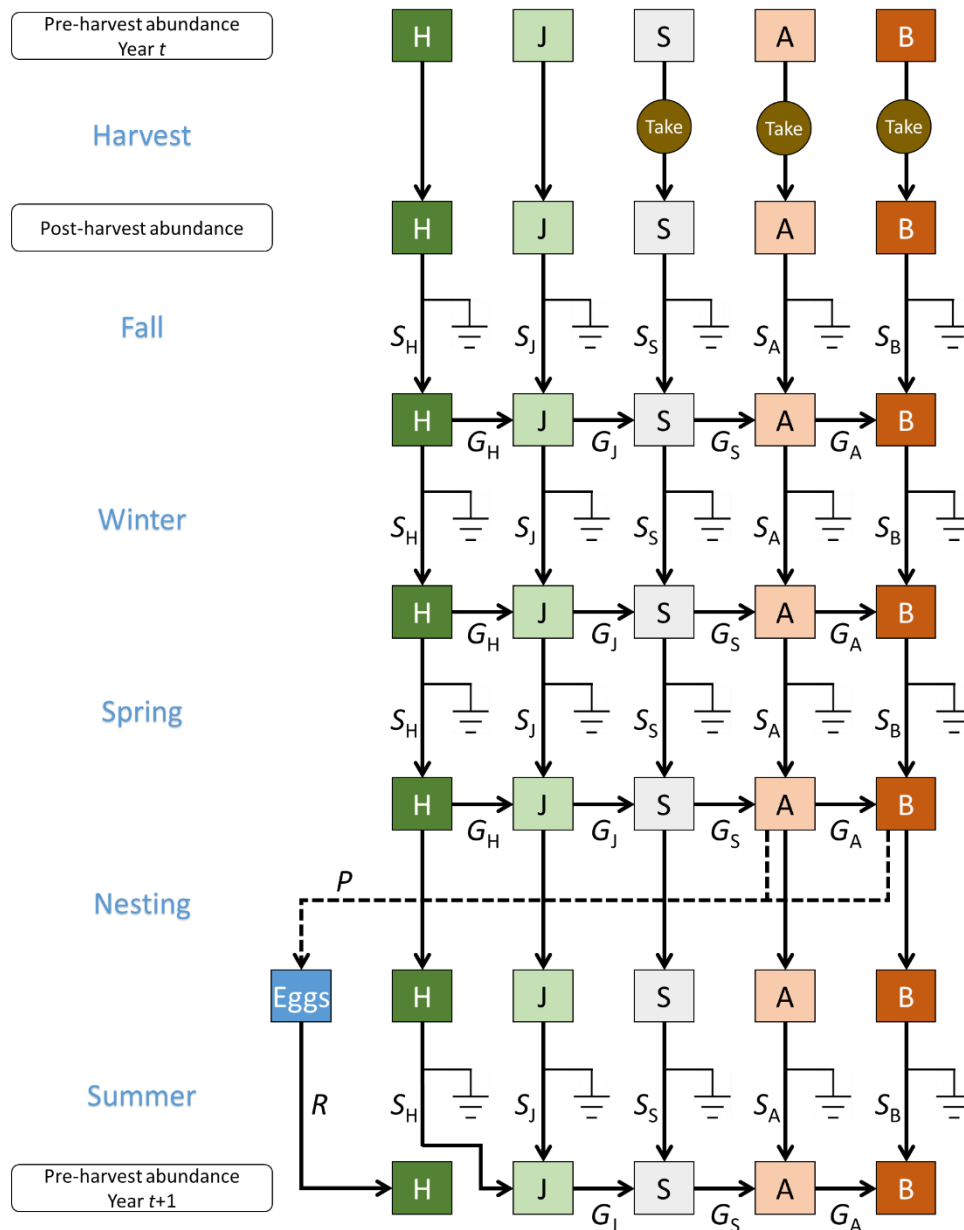


Figure 1. Flow diagram of the annual cycle of the population model, which follows individual alligators through 5 size-stage classes: hatchling (H), juvenile (J), subadult (S), adult (A), and bull (B) (sex of the alligator is also maintained in the model). The year is divided into 6 seasons where processes of harvest, survival, growth, and productivity occur. Each rate of quarterly survival ( $S_k$ ) is held at a stage-specific fixed rate, or may optionally vary in response to abundance in segments of the post-harvest population. Quarterly transitions among size classes ( $G_k$ ) are informed by a sex-specific growth model. Female alligators in the adult and bull size stages produce eggs at a rate ( $P$ ) that depends only on female size, or at a rate that varies in response to both female size and post-harvest abundance. Eggs then become hatchlings at a fixed rate of recruitment ( $R$ ).

The model included user-set switches to activate various optional forms of compensatory survival and productivity. Under no compensatory survival, quarterly rates of non-harvest mortality were held at fixed rates for hatchlings (0.200), juveniles (0.042), subadults (0.038), adult females (0.033), adult males (0.016), and bulls (either sex; 0.047), derived from annual rates used by Woodward (1996). However, non-harvest mortality rates for any of these sex-size stages could be made to vary as a logistic function of segments of the post-harvest population. Estimates of annual stage-specific survival rates and densities of alligators on Orange Lake (Woodward et al. 1992; Woodward 1996) were used to

parameterize logit-linear models that served as the compensatory functions. For hatchlings and juveniles, survival was a negative function of post-harvest density of adults and bulls. For subadults, survival was a negative function of post-harvest abundance of subadults. For adult females and adult males, survival was a negative function of pre-harvest abundance of all adults minus the fractional amount of adult harvest represented in the proportion of pre-harvest adult abundance to pre-harvest abundance of all alligators of harvestable size. For bulls (either sex), survival was a negative function of pre-harvest abundance of bulls minus the fractional amount of bull harvest represented in the proportion of pre-harvest bull abundance to pre-harvest abundance of all alligators of harvestable size. Under no compensatory productivity, the probability that a non-reproductively mature female in the adult stage ( $TL \geq 183$  cm) becomes reproductively mature is an increasing function of total length, ranging from 0.63 at  $TL = 183$  cm to 0.99 at  $TL = 274$  cm (Woodward et al. 1992). We used published estimates of maturity probability and densities of alligators on Orange Lake (Woodward et al. 1992; Woodward 1996) to parameterize a logit-linear model for a compensatory response in size at maturity. If the switch for compensatory productivity is set, the height of the size-based maturity curve varies with post-harvest adult density. At densities below 0.288 adults/ha, probabilities of reproductive maturity given total length are greater than the corresponding baseline (non-compensatory) values; at densities above 0.288 adults/ha, the opposite is true.

The first season of the year is the fall hunt. All alligators in the harvestable size stages (subadult, adult, bull) are subject to harvest at a probability specific to size stage, and non-harvest mortality during this season is assumed to be zero. The number harvested in each sex and size stage is determined as an outcome of a binomial draw with probability equal to the corresponding harvest rate. Post-harvest abundances are tallied for use in the functions for compensatory survival and productivity. For each alligator surviving the harvest, a random value drawn from a size and sex-specific growth model (Wilkinson et al. 2016) is assigned to represent the animal's growth increment in total length assuming that it survives the year; the annual increment is apportioned across seasons and is applied each season that the alligator survives.

Seasons 2, 3, and 4 are the fall, winter, and spring seasons that follow harvest and precede nesting. In each season, alligators in each sex-size stage are subject to either a fixed rate of non-harvest mortality, or to a rate that varies with certain post-harvest abundances according to the compensatory functions activated. A draw from a binomial distribution with probability equal to non-harvest mortality determines the number of alligators dying in each sex-size stage within the season. Those surviving grow a season-specific incremental amount of total length. Seasonal dynamics are executed in successive order, and we assume that the mortality processes are independent and do not vary among seasons.

The fifth season is the period of nest laying that follows the spring season and precedes the summer season. Every female in the adult and bull stages that has not achieved reproductive maturity is assigned to reproductive maturity status based on a binomial draw with a probability based on an increasing function of total length. Under compensatory productivity, the probability is also negatively dependent on the post-harvest adult density. Of those females who have reached maturity, a binomial draw with probability 0.398 (Woodward 1996; Appendix A) determines how many will produce a nest. In every nest produced, a Poisson draw with mean 32.8 (Woodward 1996; Appendix A) determines clutch size. Finally, a binomial draw with probability 0.406 – which reflects a combined rate of nest success, egg viability, and recruitment into the hatchling stage (Woodward 1996; Appendix A) – determines number of young emerging from the nest and entering the fall population as hatchlings. A sex is assigned to each new alligator based on a binomial draw with probability 0.5, and an initial total

length is assigned based on a draw from a truncated normal distribution ( $\mu = 20$ ,  $\sigma = 3$ ,  $[18, 24]$ ). During this season, non-harvest mortality is assumed to be zero for all sex-size stages.

The last season of the year is summer in which non-hunting mortality is applied across all sex-size stages and all surviving alligators are grown. As in the fall, winter, and spring seasons, alligators are subject to a fixed rate of non-harvest mortality, or to a rate that varies according to the compensatory functions activated. Alligators survive according to binomial draws, and the survivors grow according to their summer season growth increment.

We simulated the model over a 214-year time horizon (1801 – 2014) from a common starting distribution of 1000, 1032, 376, 369, and 353 in the hatchling, juvenile, subadult, adult, and bull size stages, respectively. In some of our model runs, we simulated a harvest at a target harvest rate of 0.135 applied to each harvestable size stage for the years 1981-2014, the years that legal harvest of alligators resumed on Orange Lake following federal listing of the species. In no scenario where some form of density dependence in either survival or productivity was not considered, the simulated (non-hunted) population was extirpated in 100-150 years (Figure 2).

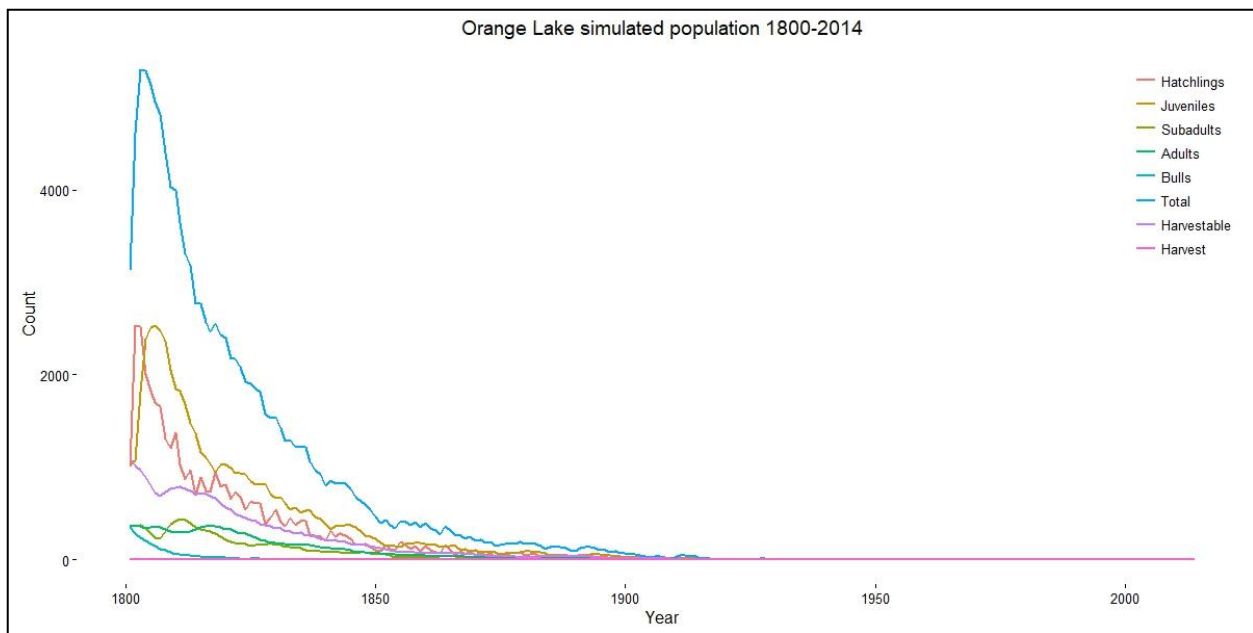


Figure 2. Simulation of the Orange Lake alligator population, with no form of density dependence in survival or productivity

Henceforth, we report results of populations simulated under some form of density dependence. We simulated a non-hunted population under each of the six forms of density-dependent survival, applying each one in turn. Density-dependent forms of hatchling survival, juvenile survival, and adult female survival yielded stable populations over the 214-year time frame, with the hatchling survival version exhibiting cyclic generational patterns approximately every 20 years (Figure 3).

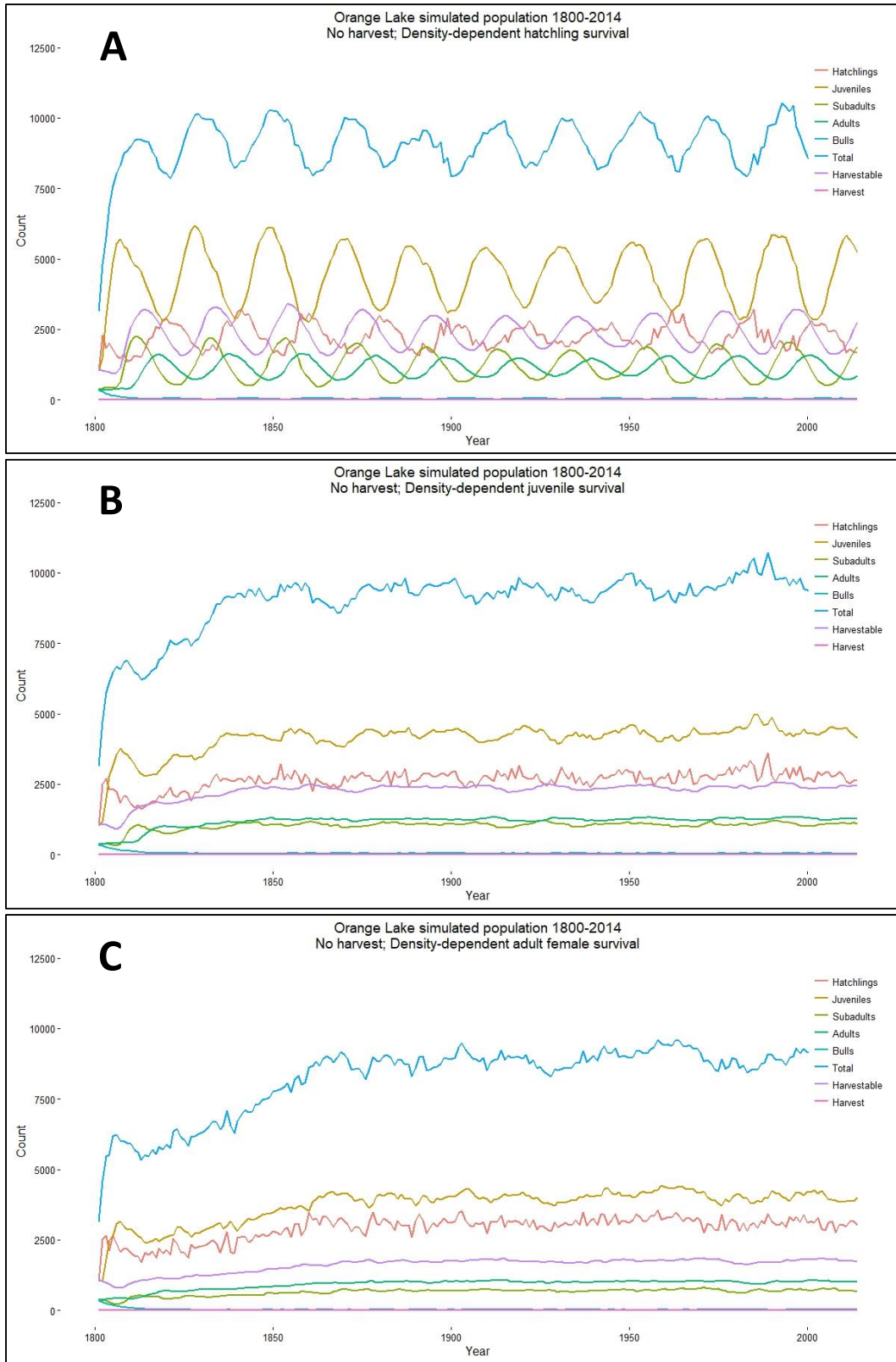


Figure 3. Forms of compensatory survival, applied to the hatchling (A), juvenile (B), and adult female (C) segments of the population, in the absence of hunting.

Density dependence in subadult survival, adult male survival, and bull survival were not sufficient by themselves to sustain the population. Density dependence in the productivity response alone also led to population extirpation (Figure 4).

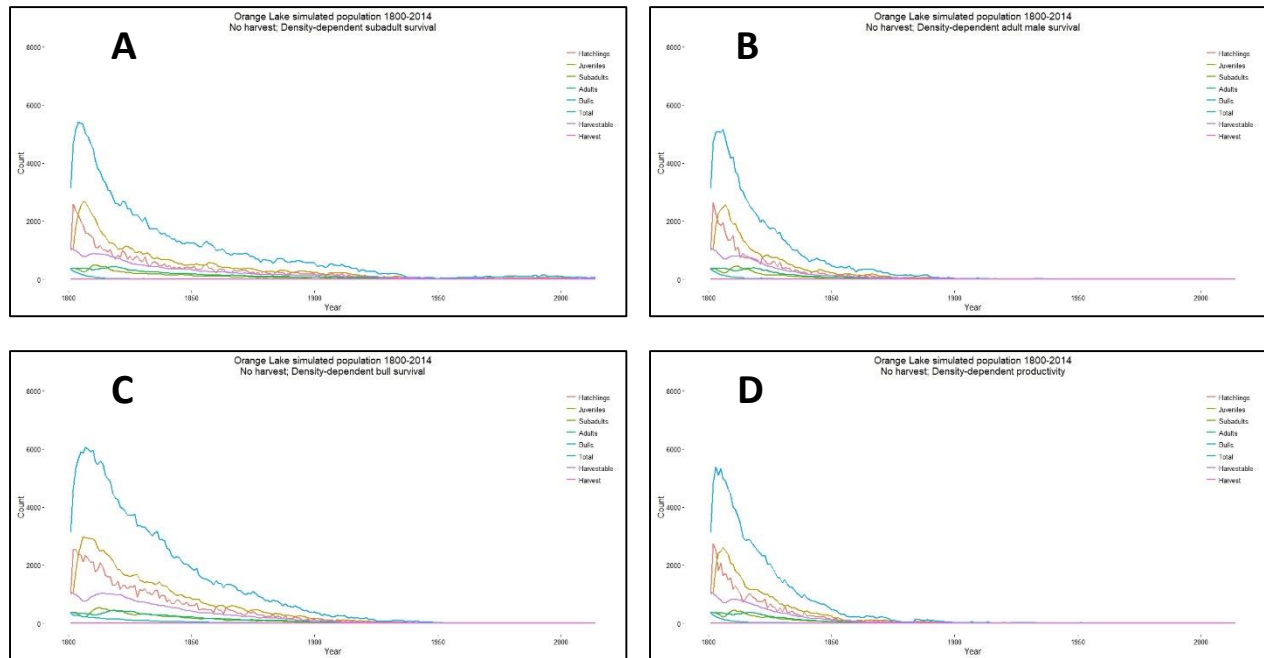


Figure 4. Forms of compensatory survival applied to the subadult (A), adult male (B), and bull (C) segments of the population, and compensatory productivity (D), in the absence of hunting.

We simulated a non-hunted population under many different combinations of density-dependent mechanisms. In most cases, combinations of mechanisms produced one of the stable patterns above, but two combinations (juvenile and subadult survival; subadult and adult female survival) produced abundance patterns that appeared to be most biologically reasonable, based on measured densities of alligators on Orange Lake (Figure 5). However, these two forms of density dependence could not sustain the population when harvest was simulated (Figure 6). We found that harvest could be sustained under either model only when a density dependent response in hatchling survival was included (Figure 7).

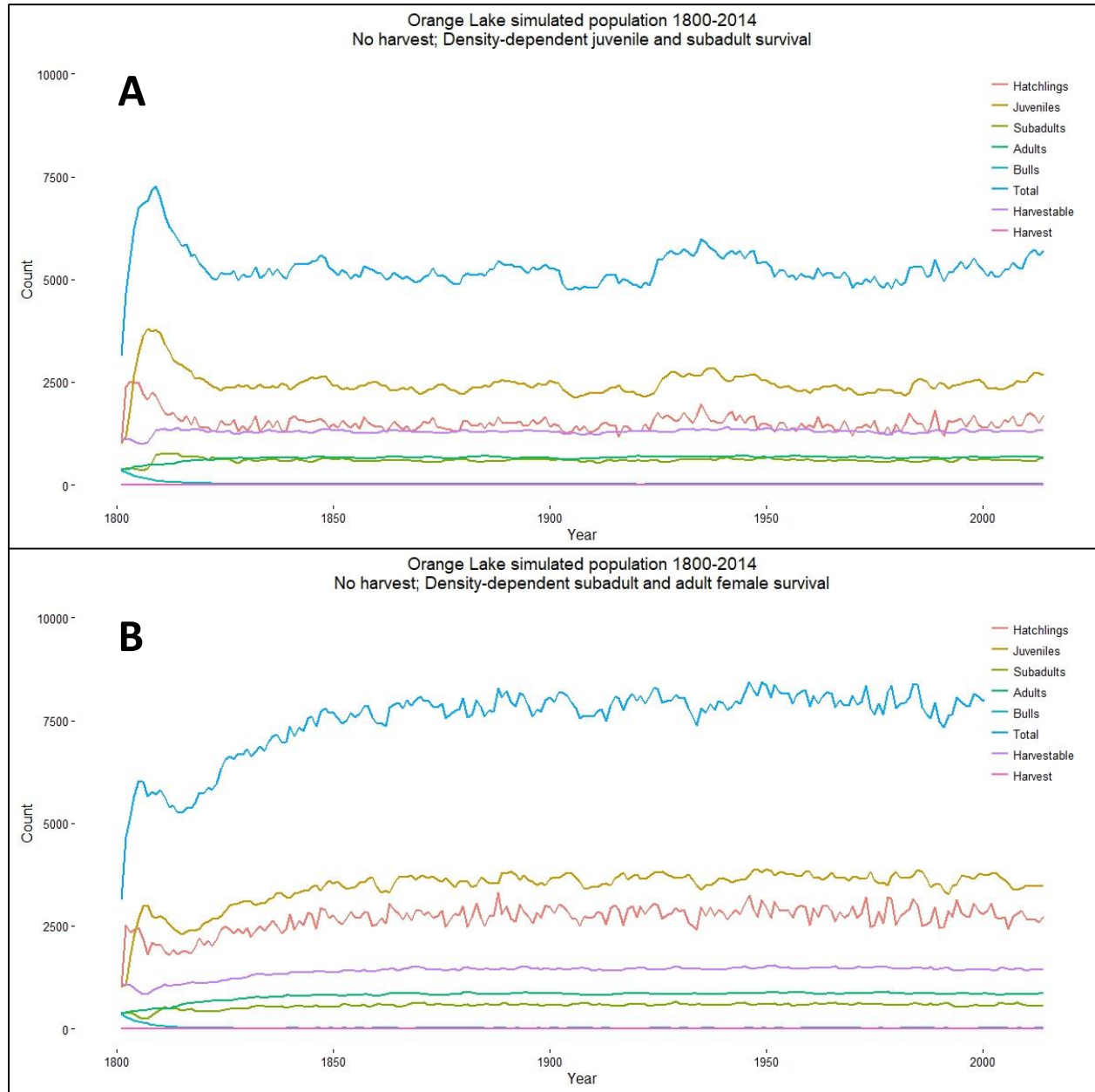


Figure 5. Simulation of population under compensatory survival in the absence of hunting for both juveniles and subadults (A) and for both subadults and adult females (B).

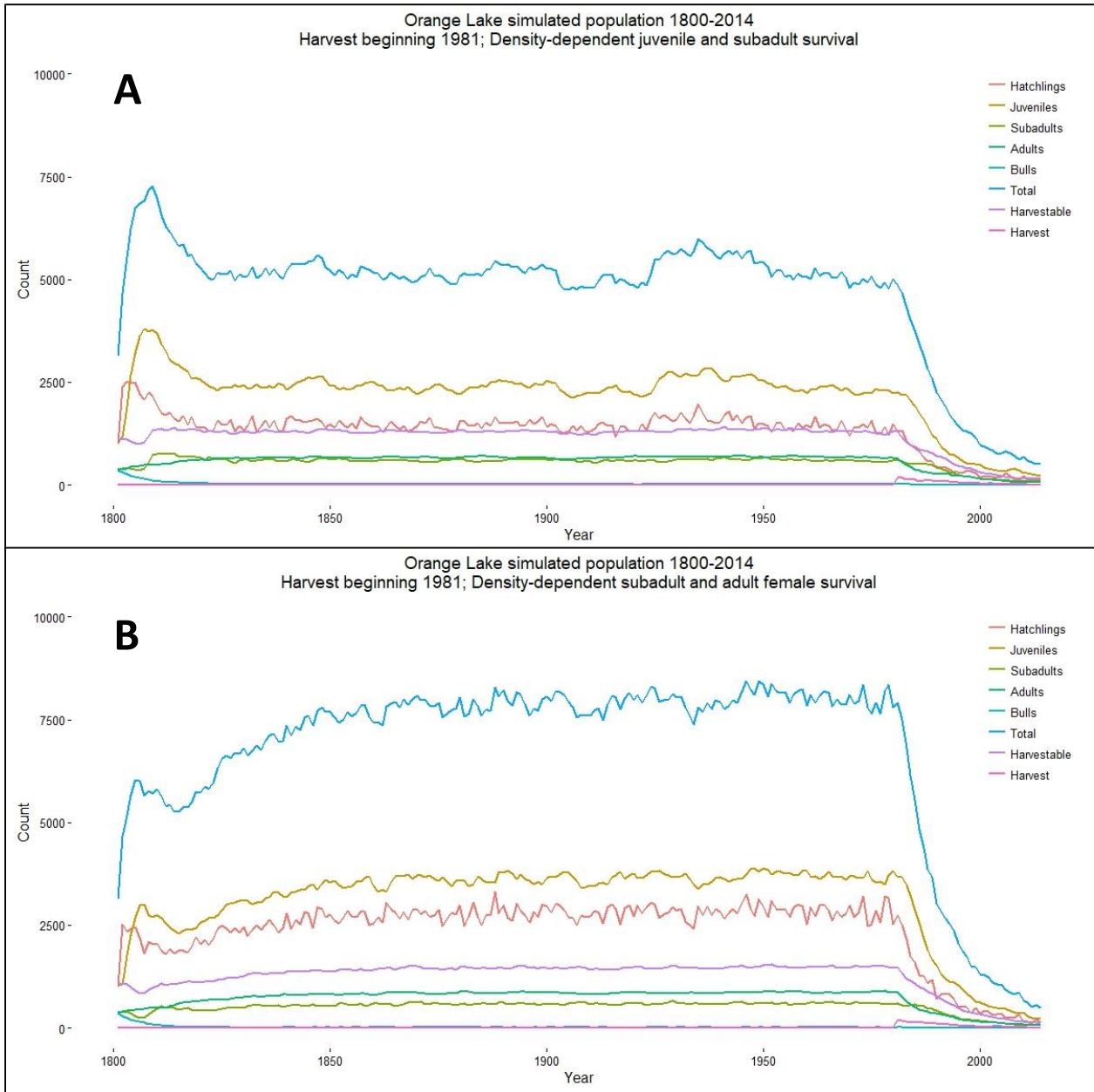


Figure 6. Simulation of population under compensatory survival in the presence of hunting (beginning 1981) for both juveniles and subadults (A) and for both subadults and adult females (B).

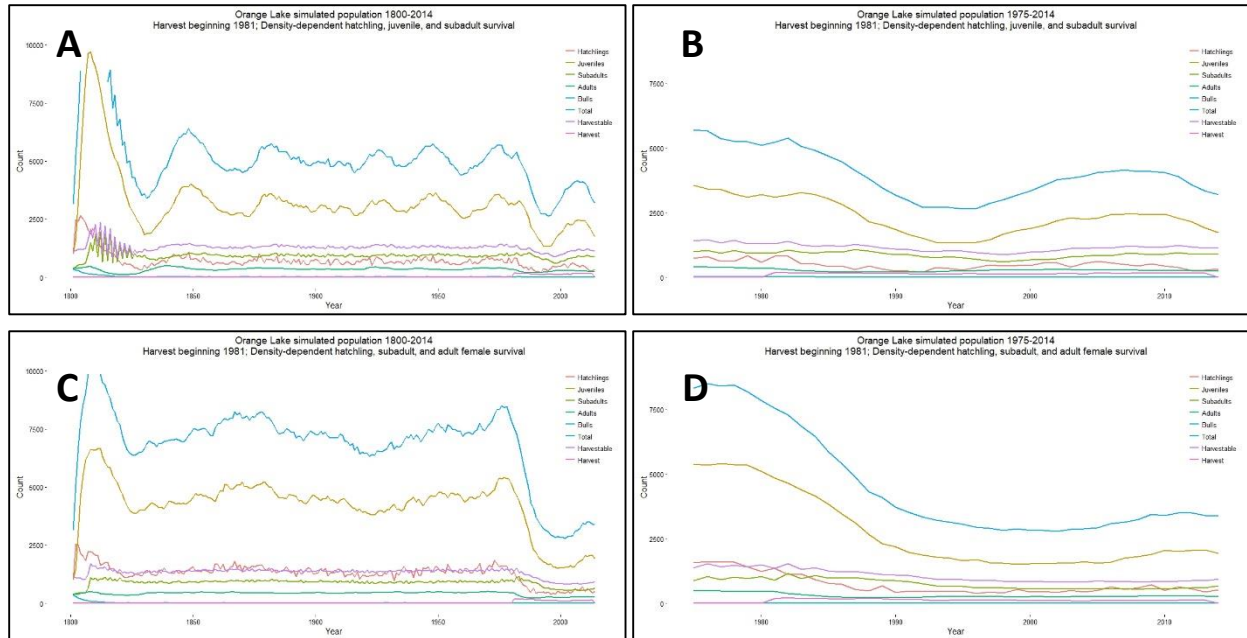


Figure 7. Simulation of population in the presence of hunting (beginning 1981) under compensatory survival for hatchlings, juveniles, and subadults (A, B) and for hatchlings, subadults, and adult females (C, D).

## Future Steps

As mentioned earlier, our simulation model for Orange Lake was built on values derived from the literature and unpublished reports. The model is static in the sense that parameters are unresponsive to additional information presented to the model. Ultimately, we will build and parameterize a population model that integrates direct observational data from multiple sources, including capture of marked alligators, egg collection efforts, population surveys, and harvest records. Unlike the current model, data from each source will inform underlying parameters of survival and productivity. Because an integrated model tracks the latent population state through time, parameters within the model are structurally interconnected. Thus, parameters across the model are responsive to the presentation of more data from any source or all sources.

Our next task is to use the simulation model demonstrated above to generate random sets of data of the kind that are routinely collected in population studies and in harvest management and that could be exploited in the construction of an integrated model. We will build the structure of an integrated model (Figure 8), and we will use the simulated data to estimate parameters within the IPM. We will validate our work by comparing estimated parameters in the IPM to corresponding parameters in the model that generated the data. Finally, we will fit the IPM to real data collected in the field at Orange Lake.

After assessing that the resulting model exhibits reasonable behavior and predicts sources of data not used to build the model, we will couple the model with a mathematical statement of harvest objectives and use stochastic dynamic programming to search for a stationary, sustainable harvest policy. We will explore sensitivity of the policy to different assumptions about mechanisms that remain uncertain to us, perhaps prompting a search for an active adaptive optimal policy.

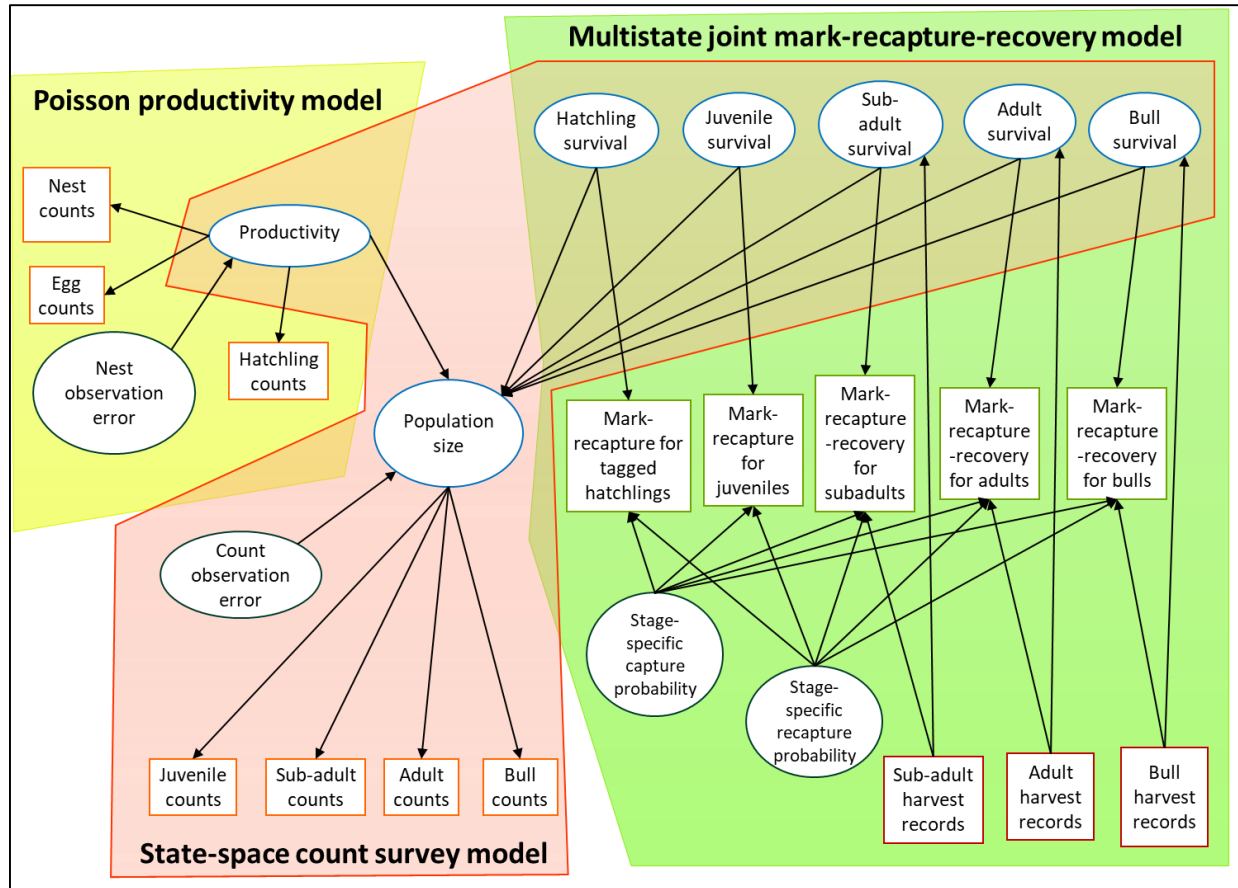


Figure 8. Schematic illustration of a population model that integrates common sources of data to jointly estimate parameters of survival (mark-recapture and harvest records), productivity (counts of nests, eggs, and hatchlings), and abundance (night-light survey counts).

Finally – based on the stakeholder workshop results – we will consider how to adapt biological structure and sampling structure within the model to represent populations in other parts of the range. By coupling these model variations with local statements of harvest objectives, we may be able to derive optimal decision policies for other ecological and political subdivisions of the range.

### Student Development

This project provided material support (computer, travel, supplies) to Ms. Tara Gancos Crawford, a PhD candidate in the Warnell School of Forestry and Natural Resources at the University of Georgia. Activities conducted under this project include presentations, workshops, symposia, and media contributions. Ms. Gancos Crawford also received several honors while supported by the project.

#### Student-led Presentations

- Crawford, T. G., and C. T. Moore. 2013. Population modeling and development of decision support tools for public alligator harvest. Georgia Chapter of The Wildlife Society. 5-6 September 2013, Athens, GA.
- Crawford, T. G., and C. T. Moore. 2014. Statewide adaptive management of public alligator harvests using structured decision making and integrated population modeling. 23rd Working Meeting of the IUCN-SSC Crocodile Specialist Group, 26-30 May 2014, Lake Charles, LA.

- Crawford, T. G., and C. T. Moore. 2014. Toward an integrated population model for support of American alligator harvest decision making. 68th Annual Conference of the Southeastern Association of Fish and Wildlife Agencies, 19-22 October 2014, Destin, FL.
- Crawford, T. G., C. T. Moore, G. Balkcom, A. M. Brunell, T. Brunjes, J. Butfiloski, C. Carter, H. Dutton, N. Heynen, C. Nix, R. Tharp, G. Waters, and A. Woodward. 2015. Agency approaches to management of public alligator harvest programs in the species' eastern range. Annual Meeting of the Southeastern Association of Fish and Wildlife Agencies, 1-4 November 2015, Asheville, NC.
- Crawford, T. G., B. Crawford, C. T. Moore, and N. Heynen. 2016. Structured decision making as a process catalyst for integrative thinking and collaboration. The Wildlife Society 23rd Annual Conference, 15-19 October 2016, Raleigh, NC.

#### Media Contributions

- Unattributed contribution. 2013. Alligator research efforts assisting states in harvest management. Feature article in "Cooperative Research Unit Corner", Outdoor News Bulletin, September 2013, <http://wildlifemanagement.institute/outdoor-news-bulletin/september-2013/alligator-research-efforts-assisting-states-harvest-management>.
- Unattributed contribution. 2017. Turning uncertainty into useful information for conservation decisions. Feature article in "Cooperative Research Unit Corner", Outdoor News Bulletin, April 2017, <http://wildlifemanagement.institute/outdoor-news-bulletin/april-2017/turning-uncertainty-useful-information-conservation-decisions>.

#### Peer-reviewed Publications

- Irwin, B. J., B. A. Crawford, T. Gancos Crawford, and C. T. Moore. 2016. Turning uncertainty into useful information for conservation decisions. Southeast Climate Science Center Fact Sheet 2016-02, [https://globalchange.ncsu.edu/secsc/wp-content/uploads/SECSC\\_FactSheet\\_2016\\_02\\_Final.pdf](https://globalchange.ncsu.edu/secsc/wp-content/uploads/SECSC_FactSheet_2016_02_Final.pdf)

#### Workshops and Symposia

- Co-organizer of a stakeholder decision-structuring workshop "Decision Support for Public Alligator Harvesting in the Southeast," Brunswick, GA, 17-19 December 2013.
- Co-organizer of a stakeholder decision-structuring workshop "Decision Support for Public Alligator Harvesting in the Southeast," Newton, GA, 16-17 December 2014.
- Co-organizer of symposium "Applications of Decision Analysis for Wildlife Population Management," The Wildlife Society 23rd Annual Conference, 15-19 October 2016, Raleigh, NC.
- Co-organizer of symposium "Structured Decision Making: A Vehicle for Navigating the Crossroads of Cultures in Wildlife Management," The Wildlife Society 24th Annual Conference, 23-27 September 2017, Albuquerque, NM.

#### Development Activities

- Structured Decision Making Workshop – Observers and Mentees, USFWS - National Conservation Training Center, 9-13 February 2015.

#### Awards and Honors

- 1st Place Student Presentation Award, Georgia Chapter of The Wildlife Society, 9 September 2013.
- 3rd Place Ph.D. Student Presentation Award, Warnell School of Forestry and Natural Resources, Graduate Student Symposium, UGA, 21 February 2014.

Three Minute Thesis (3MT™) Competition Finalist, The Graduate School, UGA, 2 April 2014, <http://grad.uga.edu/index.php/current-students/professional-development/3mt/2014-3mt-results/>.

1st Place Ph.D. Student Presentation Award, Warnell School of Forestry and Natural Resources, Graduate Student Symposium, UGA, 20 February 2015.

Archie E. Patterson Endowed Scholarship, Warnell School of Forestry and Natural Resources, UGA, 9 April 2016.

Martha Love May Memorial Scholarship, Warnell School of Forestry and Natural Resources, UGA, 22 April 2016.

Rotary Deans' Service Award for the Warnell School of Forestry and Natural Resources, UGA Rotaract Club and Rotary Club of Athens, 11 May 2016.

UGA Amazing Student Feature, University of Georgia, 29 May 2016, <http://www.uga.edu/amazing/profile/gancos-crawford-tara/>.

Sisson Community Leadership Development Award (Student), JW Fanning Institute of Leadership Development, University of Georgia, 28 April 2017.

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Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152 (Supplement 1):S227-S237.

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Wilkinson, P. M., T. R. Rainwater, A. R. Woodward, E. H. Leone, and C. Carter. 2016. Determinate growth and reproductive lifespan in the American alligator (*Alligator mississippiensis*): evidence from long-term recaptures. *Copeia* 104:843-852.

Williams, B. K. 1989. Review of dynamic optimization methods in renewable natural resource management. *Natural Resource Modeling* 3:137-216.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, CA.

Woodward, A. R., C. T. Moore, M. F. Delany. 1992. Experimental alligator harvest. Final Report, Study Number 7567. Florida Game and Fresh Water Fish Commission, Tallahassee, 118pp.

Woodward, A. R. 1996. Determination of appropriate harvest strategies for alligator management units. Final Report, Study Number 7562. Florida Game and Fresh Water Fish Commission, Tallahassee, 29 pp plus 5 appendices.

**Appendices**

- A. Pre-workshop questionnaire distributed to stakeholders (2013)
- B. Agendas for stakeholder workshops (2013, 2014)
- C. Comparison of public alligator harvest programs in Alabama, Florida, Georgia, and South Carolina, current as of the 2015 hunting season.

**Public Alligator Harvest Decision Support Project**  
**Agency Pre-Workshop Questions**

Purpose: One of the purposes of our upcoming face-to-face meeting is to understand aspects of your agency's alligator harvest management and monitoring program. We would like to understand how your program works, what goes into regulation setting, and your perspectives on challenges in its implementation. Additionally, we would like to assess differences and commonalities in harvest management programs across the range of our project. Therefore, our discussions will be largely structured around the set of questions below. We are providing the questions to you at this time so that you can consider how you would like to respond in the meeting. You may find it helpful to write out your responses on paper and refer to these notes at the meeting. Provide as much detail as will be helpful; if there is a publication that provides an adequate response for a question, feel free to provide that to us and simply refer us to that material. If you do choose to write out responses and don't mind sharing them with us, we will keep that material confidential.

Thanks in advance for your help!

Clint Moore and Tara Gancos Crawford

Harvest Management Program

1. What do you want to achieve through your alligator harvest management program? Please list all of the goals of your program. Are there any goals not "on paper"?
2. Why is alligator harvest management important? That is, what are the reasons that make this preferable to either no harvest at all or to unregulated harvest?
3. Are there separate public and private lands harvest programs? Are there different processes for setting regulations in the two programs?
4. What components of the alligator population are harvested (e.g., eggs, hatchlings, specific size classes)?

5. What policy/regulatory actions are used currently? That is, list the full range of quotas, season lengths, etc., from which different regulatory actions are formed.
  - a. Are there policy/regulatory alternatives that are not part of the program that you are interested in pursuing? Why?
  - b. What regulatory constraints exist (i.e., some options that might be useful but are not logistically or politically feasible)?
6. How are harvest decisions made?
  - a. Who makes the ultimate harvest decision, and who may veto or otherwise modify the decision?
  - b. How do you choose among alternative actions?
  - c. Are different harvest actions selected for different zones or populations?
  - d. What is the timeline for making harvest management decisions each year?
7. What makes choice of an action difficult? Consider each of the following aspects:
  - a. Lack of clarity related to the objectives of the program (either identifying them or trading off among conflicting ones)?
  - b. Uncertainty related to population biology (how populations respond to harvest)?
  - c. Uncertainty related to the connection between the population and what is monitored?
  - d. Any other uncertainties?
8. Are you satisfied with the current harvest program?
  - a. If so, what aspects of the program do you want to maintain? Why?
  - b. If not, what aspects do you think can or should be improved? Why? How?

### Monitoring Program

9. How is monitoring and harvest data incorporated into the harvest regulation decision process (i.e., how do data support decision-making)?
  - a. What information is considered when setting regulations each year?
  - b. When is that information collected relative to when it is used for management?
  - c. How is the information collected?
10. What information/data do you have about the alligator population you manage?
  - a. What type of data do you have?
  - b. What is the spatial coverage of your data?
  - c. What is the temporal coverage of your data?
  - d. Who is responsible for collecting monitoring data? Harvest data?
11. How well do you think the monitoring program assesses the populations you are harvesting, and what factors make monitoring difficult?

### General

12. In your experience, intuition, or opinion, what are areas of uncertainty regarding your alligator population and its management that you think need to be addressed?
13. What do you and your agency hope to get out of this project?
14. Do you have a timeline for your engagement or the production of outcomes that we should be aware of?



**Daniel B. Warnell School of Forestry and Natural Resources**  
Forestry, Wildlife, Water and Soil Resources, Fisheries and Aquaculture,  
Natural Resource Recreation and Tourism

## **DECISION SUPPORT FOR PUBLIC ALLIGATOR HARVESTING IN THE SOUTHEAST**

### **Decision Structuring Workshop Agenda**

December 17-19, 2013

Georgia Department of Natural Resources, Coastal Regional Headquarters Office  
One Conservation Way, Brunswick, Georgia 31520

#### **Tuesday, December 17, 2013**

##### **9:00 am – Module 1: Problem Definition**

- Presentation: Decision context and overview of outcomes from individual meetings with states
- Discussion: Pertinent scales and resolution of management objectives and strategies

**12:00 pm – LUNCH BREAK**

##### **1:00 pm – Module 2: Objectives**

- Round 1: Construct state-specific objective hierarchies; distinguish fundamental and means objectives; identify strategies for dealing with competing objectives
- Discussion: Round 1 outcomes
- Round 2: Revise objective hierarchies and decide criteria for evaluating competing objectives

**3:00 pm-5:00 pm – Module 3: Management Alternatives (Discussion)**

#### **Wednesday, December 18, 2013**

##### **9:00 am – Module 4: Population Models**

- Presentation: Outcomes of 2010 Adaptive Management Conference Series Meeting
- Discussion: Existing models and their potential use

**10:00am – Module 5: Influence Diagrams (Group Activity)**

**12:00pm - LUNCH BREAK**

**1:00pm-5:00pm – Module 6: Monitoring Strategies and Survey Design (Discussion)**

#### **Thursday, December 19, 2013**

##### **9:00 am – Module 7: Rapid Prototyping (Exercise)**

- Review and revision of objectives, alternatives, and influence diagrams

**12:00 pm - LUNCH BREAK**

##### **1:00 pm – Meeting Wrap-Up**

- Presentation: Integrative research ideas and discussion
- Discussion: Sharing and crediting data
- Define participant responsibilities

**3:00 pm – Meeting Adjournment**



**Daniel B. Warnell School of Forestry and Natural Resources**  
Forestry, Wildlife, Water and Soil Resources, Fisheries and Aquaculture,  
Natural Resource Recreation and Tourism

## **DECISION SUPPORT FOR ALLIGATOR HARVEST PROGRAMS IN THE SOUTHEAST**

### **Collaborator Workshop Agenda December 16-17, 2014**

J.W. Jones Ecological Research Center, Newton, Georgia

#### **Objectives:**

- Touch base, update on progress
- Develop conceptual model for generic population, at survey-unit and regional/landscape scales
- Identify key uncertainties and expectations for their resolution

#### **Tuesday, December 16, 2014**

##### **8:00 am – Module 1: Status Update, Progress**

- Progress on model-building aspect – trying to figure out how to integrate multiple sources of data into comprehensive pop model; simulation process/approach
- Compilation of state alligator management programs (notes update; cross-agency comparison)
- Areas of development via coursework: math and biology, SDM and AHM, human dimensions (ICON), etc.

##### **9:00 am – Module 2: Overview of our synthesis from modelling activity last workshop**

- Group conceptual diagram editing activity - focus on biological realism of generic population

##### **12:00 pm – LUNCH BREAK**

##### **1:00 pm – Module 3: Refine and simplify conceptual diagram**

- What are the factors that we need to include in our model? (Group exercise)

##### **3:00-5:00 pm – Module 4.1: What aspects of the survey-unit population model do we model?**

#### **Wednesday, December 17, 2014**

##### **8:00 am – Module 4.2: What uncertainties exist, and what kind are they?**

- Group Exercise – Consider aspects of uncertainty in a survey-unit population model; can any be reduced by data over time?: (1) structural uncertainty, (2) partial controllability, (3) environmental stochasticity, (4) partial observability

##### **10:00 am – Module 5: Regional/landscape scale (model) considerations (latitude, physiography, etc.)**

- Group Exercise

##### **11:30 am – Wrap-up:**

- Discussion of cross-agency comparison document corrections
- Discuss value/interest/comfort with publishing cross-state comparison...
  - Can this be shared, and what level of detail (if so)?
  - What about publishing (and how we frame it)?

##### **12:00 pm – Adjourn**

	Florida Fish and Wildlife Conservation Commission (FWC)	Georgia Department of Natural Resources (GADNR)	Alabama Department of Conservation and Natural Resources (ALDCNR)	South Carolina Department of Natural Resources (SCDNR)
<b>Population size</b>	~ 1.3 million (2014)	~ 222,000 (2010)	Unknown	~ 100,000 (2014)
<b>Management programs for wild alligators<sup>1</sup></b>	Nuisance control (1978) Public recreational harvest <sup>2</sup> (1988) Private lands (1988)	Nuisance control (1980) Joint public/private recreational harvest <sup>3</sup> (2003)	Nuisance control (1990) Joint public/private recreational harvest <sup>4</sup> (2006)	Nuisance control (1987) Public recreational harvest <sup>5</sup> (2008) Private lands (1995)
<b>Program guidance</b>	Alligator Management Plan (1984); Alligator Management Program Proposal (1985); Measureable Goals and Objectives (2006)	<a href="#">Alligator Management Plan</a> (2010)	Not formalized	Not formalized
<b>Management units</b>	68 public water body-specific units <sup>6</sup> 65 county-wide units <sup>7,8</sup>	9 county/watershed-based zones <sup>9</sup>	3 specific geographic zones <sup>10</sup>	4 broad geographic units <sup>11,12</sup>
<b>Season</b>	Permittees <sup>13</sup> assigned to one of four 7-day harvest periods between mid-August – mid-September <sup>14,15</sup>	1 <sup>st</sup> Saturday in September – 1 <sup>st</sup> Sunday in October	Zone-specific: Two weekends in mid-late August (SW, WC); two full weeks in mid-August (SE) <sup>16</sup>	2 <sup>nd</sup> Saturday in September – 2 <sup>nd</sup> Saturday in October <sup>17</sup>
<b>Daily hunt hours</b>	5:00pm - 10:00am	12:00pm - 12:00pm	8:00pm - 6:00am	12:00pm - 12:00pm
<b>Statewide permit quota</b>	5,886 permits, variably allocated among units <sup>18</sup>	850 permits, variably allocated among zones	240 permits, variably allocated among zones	1,000 permits, evenly distributed among units <sup>19</sup>

<sup>1</sup> With the exception of first two rows, information provided in this table is specific to the public (FL, SC) and joint public/private (GA, AL) recreational harvest program in each state. Information contained herein is current as of the 2015 hunting season unless noted otherwise.

<sup>2</sup> [Florida Fish and Wildlife Conservation Commission \(FWC\) Statewide Alligator Harvest Program](#)

<sup>3</sup> [Georgia Department of Natural Resources \(GADNR\) Alligator Hunting Season](#)

<sup>4</sup> [Alabama Department of Conservation and Natural Resources \(ALDCNR\) Alligator Hunting Season](#)

<sup>5</sup> [South Carolina Department of Natural Resources \(SCDNR\) Alligator Hunting Season](#)

<sup>6</sup> **FWC:** Includes six [Stormwater Treatment Area Alligator Harvest Units](#) and Loxahatchee National Wildlife Refuge (added in 2014)

<sup>7</sup> **FWC:** Applies to areas within specific counties, excluding public water bodies designated as water body-specific alligator harvest units (AHUs)

<sup>8</sup> **FWC:** [Alligator Harvest Units, Map and Quotas](#)

<sup>9</sup> **GADNR:** [Alligator Season Hunt Zones and Quotas Map](#)

<sup>10</sup> **ALDCNR:** Mobile-Tensaw Delta (Southwest, SW zone; established 2006), Southeast (SE zone; established 2007); West-Central (WC; established 2011)

<sup>11</sup> **SCDNR:** [Alligator Management Units](#); Hunting is limited to public waters within groupings of counties across the coastal plain region, excluding waters in Wildlife Management Areas (WMAs) or US Fish and Wildlife Service (USFWS) Refuges, and private lands not participating in the Private Lands Alligator Program but for which permission has been granted to the permittee.

<sup>12</sup> **SCDNR:** A special *WMA Alligator Hunt* involving its own set harvest rules regulations is embedded within the larger alligator harvest management units, including designated areas within two WMAs (Bear Island WMA and Santee Coastal Reserve WMA).

<sup>13</sup> **FWC:** Also referred to as “trappers”

<sup>14</sup> **FWC:** (1) August 15-22, 2014; (2) August 22-29, 2014; (3) August 29-September 5, 2014; (4) September 5-12, 2014

<sup>15</sup> **FWC:** All permittees also allowed to take alligators September 12 –November 1 if they have unused tags after end of assigned harvest period; Exceptions specified on the harvest permit

<sup>16</sup> **ALDCNR:** August 14-17 and 21-24, 2014 (SW, WC); August 8-24, 2014 (SE)

<sup>17</sup> **SCDNR:** For *WMA Alligator Hunt*, permittees assigned to one of four hunt periods between the last 3 weeks of September – 1<sup>st</sup> week of October, and they may hunt Monday – Saturday during their assigned period.

<sup>18</sup> **FWC:** Take of 2 alligators authorized per permit for a total harvest quota of 11,772 alligators

<sup>19</sup> **SCDNR:** An additional quota is allocated for the *WMA Alligator Hunt*; 16 (up to 32) permits available, two hunters assigned to each of four hunt periods within each of the two participating WMA properties. The first 16 permits allocated may be filled during the permitted hunt period within the assigned WMA *or* elsewhere within the alligator management unit encompassing the permitted WMA property during the public alligator harvest season. The additional 16 permits are

<b>Permitted bag limit</b>	2 alligators	1 alligator	1 alligator	1 alligator <sup>20</sup>
<b>Size limit</b>	Non-hatchling ( $\geq$ 18in. total length; $\geq$ 9in. snout-to-vent length) <sup>21</sup>	$\geq$ 48in. total length	Zone-specific: Non-hatchling (SW, WC); $\geq$ 8ft. total length (SE)	$\geq$ 48in. total length <sup>22</sup>
<b>Permit application process, fees, and restrictions</b>	Application: Online, at tax collector office or via worksheet submitted to license agent Application fee: None Permit fee: None Selection: 3-phases <sup>23</sup> ; Random drawing in Phases I and II, and first-come-first-served basis in Phase III Restrictions: Application in Phase II limited to customers without a permit from Phase I <sup>24</sup>	Application: Online Application fee: None Permit fee: None Selection: Priority points-based drawing Restrictions: Application limited to 1 per $\leq$ 3 total zone selections	Application: Online Application fee: \$22 <sup>25</sup> Permit fee: None Selection: Priority points-based drawing <sup>26</sup> Restrictions: Application limited to 1 per $\leq$ all 3 zones; Only Alabama residents and Lifetime Hunting License holders (resident or non-resident) may apply	Application: Online or at walk-up counter at SCDNR regional office Application fee: \$10 <sup>27</sup> Permit fee: \$100 <sup>28,29</sup> Selection: Priority points-based drawing Restrictions: Application limited to 1 per $\leq$ all 4 units; units may be ranked by applicant preference
<b>Permit specificity</b>	1 alligator harvest unit and period <sup>30</sup>	1 alligator hunt zone	1 alligator hunt zone	1 alligator management unit <sup>31,32</sup>
<b>Required license(s) and fees</b>	Permittees must possess <sup>33</sup> : 1) Alligator Trapping License <sup>34</sup> : \$272 (resident, annual), \$1022 (non-resident, annual) 2) <i>If alligator trapping agent hired to assist with hunt</i> <sup>35</sup> ,	Permittees and their assistants must possess: (1) Hunting License: \$10 (annual), \$18 (2-year) (2) Alligator Hunting License: \$50 (resident, annual); \$200 (non-resident,	Permittees and their assistants must possess: (1) Small Game Hunting License: \$17.15 (resident, annual); \$96.85 (non-resident, annual), \$59.10 (non-resident, 10-day), \$42.95	Permittees and their assistants must possess <sup>37,38</sup> : (1) Hunting License: \$12 (resident, annual), \$36 (resident, 3-year); \$125 (non-resident, annual), \$75 (non-resident, 10-day), \$40 (non-resident,

available for purchase only to hunters permitted for the *WMA Alligator Hunt* and are only valid for harvest of a 4-7ft. alligator within the permittee's assigned WMA.

<sup>20</sup> **SCDNR:** For *WMA Alligator Hunt*, 1-2 alligators; See footnote, above

<sup>21</sup> **FWC:** Wild eggs and hatchlings are collected via FWC's Private Lands Alligator Management Program contingent upon a documented minimum number of alligator nests or hatchling on participating property, or from public water bodies by licensed alligator farmers who meet specific requirements to participate in FWC's Public Waters Alligator Egg and Hatchling Collection Program.

<sup>22</sup> **SCDNR:** In *WMA Alligator Hunt*, if a second permit is purchased, only one (of two) harvested alligators  $\geq$ 48in. total length

<sup>23</sup> **FWC:** Three-phase system in place since 2014; Phase I - April 25-May 5, Phase II - May 23-June 2, Phase III - June 20-until all permits have been issued

<sup>24</sup> **FWC:** Anyone may apply for remaining unpurchased permits in Phase III

<sup>25</sup> **ALDCNR:** \$20 application fee + \$2 processing fee

<sup>26</sup> **ALDCNR:** Priority-point system began in 2014; Historically, this was a completely random drawing.

<sup>27</sup> **SCDNR:** For *WMA Alligator Hunt*, the permit drawing and preference-point system is independent of the regular public recreational harvest program and has its own \$15 application fee

<sup>28</sup> **SCDNR:** \$100 Alligator Hunting Permit fee charged to drawn resident and non-resident permit applicants.

<sup>29</sup> **SCDNR:** For *WMA Alligator Hunt*, \$500 permit fee charged to drawn residents and \$800 charged to drawn non-residents

<sup>30</sup> **FWC:** Harvest unit/period assignment is based on availability and applicant's preference ranking as indicated at the time of application

<sup>31</sup> **SCDNR:** For *WMA Alligator Hunt*, permit is WMA and hunt period-specific

<sup>32</sup> **SCDNR:** Applicants may only be selected for one alligator management unit; however, because the *WMA Alligator Hunt* is an independent permit drawing and preference-point system, individuals may apply and be awarded a permit for both hunts.

<sup>33</sup> **FWC:** Unlicensed persons may ride in the boat provided that those persons do not participate in any activity involving take of an alligator; Take of an alligator is limited to the permit holder, another person in possession of a valid Alligator Trapping License or an Alligator Trapping Agent's License.

<sup>34</sup> **FWC:** Regular Florida hunting license is not required.

<sup>35</sup> **FWC:** A licensed alligator trapper (i.e. a permittee or an Alligator Trapping License holder under FWC's Private Lands Alligator Management Program or FWC's Statewide Nuisance Alligator Program) may be hired as a guide to help with the hunt.

	Alligator Trapping Agent License: \$52 (annual) <sup>36</sup>	annual) (3) <i>If hunting on WMA</i> , WMA License: \$19 (resident, annual), \$38 (resident, 2-year); \$73 (non-resident, annual)	(non-resident, 3-day) (2) <i>If hunting on a WMA</i> , WMA License: \$17.15 (annual)	3-day) <sup>39</sup> (2) Non-resident alligator hunting fee: \$200 <sup>40,41,42</sup>
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<sup>37</sup> **SCDNR:** Only permittee may dispatch alligator, but assistants can guide, help or otherwise participate; However, in *WMA Alligator Hunt*, a second purchased tag for an alligator 4-7ft in length may be used by anyone in the hunt party provided that the original permittee is present.

<sup>38</sup> **SCDNR:** In *WMA Alligator Hunt*, permittees may have no more than 3 assistants (not including a guide)

<sup>36</sup> **FWC:** A \$62 fee is charged for additional permits issued to individuals already in possession of an Alligator Trapping License that is valid through the end of the hunting season (e.g., individuals that have been awarded more than one alligator harvest permit in a season and who have already purchased their license, or alligator trapping agents that already have a license).

<sup>39</sup> **SCDNR:** Non-resident multi-day licenses are valid for consecutive days only.

<sup>40</sup> **SCDNR:** Required of non-resident permittees and assistants, including guides

<sup>41</sup> **SCDNR:** Valid for any of the SCDNR alligator hunting programs

<sup>42</sup> **SCDNR:** Additional required license and fees for *WMA Alligator Hunt* participants: (1) WMA Permit: \$30.50 (resident, annual), \$91.50 (resident, 3-year); \$76 (non-resident, annual); (2) Second alligator tag (for alligator 4-7ft. total length): \$75 (resident and non-resident); (3) *If paid guide hired to assist with WMA hunt*: Commercial use permit (requires application with fee): \$30

<b>Permittee training</b>	Permittees mailed copy of the training and orientation manual <sup>43</sup> and encouraged to attend one of several training/orientation classes throughout the state <sup>44</sup>	Permittees mailed alligator hunt information packet	Permittees <i>required</i> to attend alligator training course in their harvest zone <sup>45,46</sup>	Permittees may attend optional alligator hunting seminar <sup>47</sup>
<b>Harvest/possession tags</b>	2 permanent federal CITES <sup>48</sup> tags mailed to permittee <sup>49</sup> with copy of the training and orientation manual, harvest permit, and Alligator Trapping License  Unused CITES tags must be returned along with completed harvest forms <sup>50</sup>	1 temporary alligator harvest tag mailed to permittee with harvest permit  Permanent CITES tag is attached to carcass/hide when brought for mandatory validation at GADNR Wildlife Resources Division Game Management regional office.	1 temporary alligator possession tag issued to permittee upon completion of required training course  Permanent alligator possession tag/CITES tag attached to carcass upon mandatory validation at ALDCNR Wildlife and Freshwater Fisheries Division check station (SW, WC) or when carcass/hide brought to district office (SE)	1 South Carolina harvest tag mailed to permittee with alligator harvest permit  Federal CITES tags must be special requested by permittee for alligators destined for sale, export, or hide processing at select processors <sup>51</sup>
<b>Legal capture and dispatch<sup>52</sup></b>	Baited hooks prohibited  Capture: Artificial lures or baited, wooden pegs less than 2in. (length) attached to a hand-held restraining line, snares, harpoons, gigs, and snatch hooks <sup>53</sup> , bows and crossbows with projectiles with attached restraining line, manually operated spears, spear guns, crossbows and bows with projectiles with attached restraining line  Dispatch: Immediately upon capture <sup>54</sup> using bang stick; Gig-equipped bang sticks and firearms prohibited	Baited hooks prohibited  Capture: Hand-held ropes or snares, snatch hooks, harpoons, gigs or arrows with attached restraining line  Dispatch: Immediately upon capture using handgun or bang stick, or by cervical dislocation <sup>55</sup> with sharp implement	Baited hooks prohibited  Capture: Hand-held snares, hand-held or rod/reel snatch hooks, harpoons with attached restraining line, and bow or crossbow fishing equipment with arrow-attached restraining line  Dispatch: Immediately upon capture using shotgun (shot size ≤ #4) or bang stick (chambered in ≥ .38 caliber)	Bait, baited hooks, set hooks, and pole hunting prohibited  Capture: Hand-held harpoons, snatch hooks, jab sticks, bows and crossbows, and gigs; line or snare/noose can be used to bring alligator to shore or alongside of boat, then hand-held snare/noose or rope restraining line must be attached <sup>56</sup>  Dispatch: Immediately upon capture <sup>57</sup> using handgun, bang stick, or cervical dislocation using a sharp implement; Rifles and shotguns prohibited <sup>58</sup>
<b>Regulatory cycle</b>	Regulatory cycle varies among units based on type of quota	Regulations set on a two-year cycle with other game	Regulations set on annual cycle with other game species	Regulations set on annual cycle independent of other

<sup>43</sup> FWC: 2014 Alligator Harvest Training and Orientation Manual

<sup>44</sup> FWC: Training/orientation classes cover alligator harvest rules and regulations, alligator hunting techniques and capture/dispatch equipment, and alligator processing procedures.

<sup>45</sup> ALDCNR: In SW and WC zones, permittees who attended training in the last 3-5 years are exempt from this requirement.

<sup>46</sup> ALDCNR: Training course covers relevant regulations, alligator hunting methods and capture/dispatch equipment.

<sup>47</sup> SCDNR: In *WMA Alligator Hunt*, permittees *required* to attend on-site orientation meeting that provides map of hunting area and hunt instructions.

<sup>48</sup> Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 1973); Alligators are protected under CITES Appendix II for species that may become threatened with extinction unless trade is controlled, including "look-alike species".

<sup>49</sup> FWC: 2 orange mercury tags also mailed to permittee if permitted for the Everglades and Francis S. Taylor WMA, or the Holey Land WMA

<sup>50</sup> FWC: Unreturned CITES tags and missing harvest forms are followed-up with law enforcement.

<sup>51</sup> SCDNR: Prior arrangements must be made with a designated SCDNR office; CITES tag replaces SC harvest tag in these circumstances

<sup>52</sup> Dispatch = take = lethal removal = killing, etc.

<sup>53</sup> Snatch hook = weighted treble hook

<sup>54</sup> FWC: Capture and release is prohibited unless non-lethal capture method used (e.g., snare, rope, snatch hook)

<sup>55</sup> Cervical dislocation = severing the spinal cord

<sup>56</sup> SCDNR: Regardless of device, restraining line must be attached to head of the device and affixed to stationary object or float

<sup>57</sup> SCDNR: Catch and release is prohibited except in cases that captured alligator is ≤4ft. total length

<sup>58</sup> SCDNR: If a projectile (i.e. bolt or arrow) breaks off in the body of an alligator and the alligator escapes, the hunter is not allowed to attempt to take another alligator.

	<p>associated with it: variable quota units (annually)<sup>59</sup>; static quota units (every 5 years); county-wide quota units (fixed)<sup>60</sup></p> <p>Process overview for variable quota units: (1) Spotlight surveys conducted by FWC personnel in Spring (May/June) or Summer (July/August) depending on harvest unit and harvest data collected late fall; (2) Data compiled and analyzed by FWC Fish and Wildlife Research Institute biologists and recommended quota level for each zone determined based on established actions zones; (3) Recommendations sent to Alligator Management Program Coordinator; (4) By delegated authority from the Executive Director of FWC, Program Coordinator modifies or approves recommendations and establishes the quota for each unit for upcoming harvest season by April 1<sup>st</sup>,<sup>61</sup></p>	<p>species<sup>62,63</sup></p> <p>Process overview: (1) Spotlight surveys conducted by GADNR personnel between May and June, and harvest data collected late fall; (2) Data compiled and analyzed by State Alligator Biologist, and results and regulatory options evaluated and discussed with the Chief of Game Management; (3) Chief makes recommendations to the Director of the Wildlife Resources Division and gets approval from the Commissioner; (4) Commissioner briefs the Board of Natural Resources regarding key elements of harvest regulations package; (5) Regulations enter public hearing/comment period; (6) Proposed regulations finalized following official vote by the Board</p>	<p>Process overview: (1) Spotlight surveys conducted by ALDCNR personnel between late June and early August, and harvest data collected late fall; (2) Data compiled and discussed by field biologists and officers, and they make regulatory recommendations to the Chief of the Wildlife Section; (3) Chief passes recommendations on to the Conservation Advisory Board; (4) Proposed changes to seasons and bag limits for upcoming season finalized by a vote by the Board in January, or promulgated by the Commissioner of ALDCNR as needed</p>	<p>game species<sup>64</sup></p> <p>Process overview: (1) Spotlight surveys conducted by short-term employee contracted by SCDNR<sup>65</sup> between July and early September, and harvest data collected late fall; (2) Data compiled and evaluated by Furbearer &amp; Alligator Program Coordinator, and regulatory recommendations sent to the Chief of Wildlife Management Section; (3) Chief presents recommendations to advisory group/supervisory committees; (4) Approved recommendations forwarded to the Board who votes regulations into statute<sup>66,67</sup></p>
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<sup>59</sup> **FWC:** Variable quotas are assigned to water body-specific alligator harvest units.

<sup>60</sup> **FWC:** County-wide quotas are only adjusted when there is a significant event or pressure to change quota level

<sup>61</sup> **FWC:** A vote by the Board of Directors not required

<sup>62</sup> **GADNR:** Alligator harvest regulations are set at the same time as regulations for all other game species, except waterfowl.

<sup>63</sup> **GADNR:** Under special circumstances, it's possible to make emergency regulations and small regulatory changes in off years.

<sup>64</sup> **SCDNR:** However, changes to alligator harvest regulations seldom occur.

<sup>65</sup> **SCDNR:** Since 2014, Clemson affiliates have helped conduct population monitoring surveys.

<sup>66</sup> **SCDNR:** Some deviation from this process occurs in practice based on managers' judgment and expertise

<sup>67</sup> **SCDNR:** Changes to harvest methodology (e.g., capture and dispatch techniques, quota level) can be made on the harvest permit itself easily; specifics of the harvest program (e.g., season) are set in statute and require the state legislature to change.

<p><b>Data considered in decision making</b></p>	<p>Variable quota units: Annual adult population size estimate for units (1988-present), environmental data associated with spotlight surveys, harvest data from most recent season<sup>68</sup>, and anticipated changes in/to the units<sup>69,70</sup></p> <p>County-wide quota units: Unit-specific habitat assessments<sup>71</sup></p> <p>Static quota units: Adult population size estimate when units established and at time of 5-year reassessment<sup>72</sup></p>	<p>Current population index value (3-year average of count per mile survey route) for zones and statewide, current reproductive index (i.e. nest count), and harvest data from the most recent season</p>	<p>Current population index value (i.e. count per hour along survey route) for zones and harvest success data from the most recent season</p>	<p>Current population index value (i.e. count per mile survey route) for units and harvest data from most recent season</p>
<p><b>Decision thresholds for adjusting number of available permits</b></p>	<p>Actions zones (green, yellow and red) set relative to pre-harvest estimates (1988): <sup>73,74,75</sup></p> <ul style="list-style-type: none"> <li>● 70% CI<sup>76</sup> overlaps green zone - quota set at 6% of current estimate adjusted for mean harvest proportions<sup>77</sup></li> <li>● 70% CI is above green zone - quota set at 12% of current estimate<sup>78,79</sup></li> <li>● 70% CI falls below green zone, but current estimate is in yellow zone - quota set at 3% of current estimate adjusted for mean harvest proportions</li> <li>● Current estimate falls within red zone - quota set to 0<sup>80</sup></li> </ul>	<p>Actions based on current population index values relative to baseline averages established with data from 1990-2009:</p> <ul style="list-style-type: none"> <li>● 50% decrease in long-term average # alligators/mile - close harvest</li> <li>● 33% decrease in long-term average # alligators/mile - restrict harvest<sup>81</sup></li> <li>● 33% increase in long-term average # alligators/mile - liberalize harvest<sup>82</sup></li> </ul>	<p>Not formalized; Conservative approach based on expert judgment</p>	<p>Not formalized; Conservative approach based on expert judgment</p>

<sup>68</sup> **FWC:** The quota for each unit is adjusted based on (1) the mean proportion of harvest in that unit over the preceding three years that consisted of adult alligators, and (2) the mean proportion of the quota for that unit taken over all years; Harvested juveniles and subadults are not taken into consideration.

<sup>69</sup> **FWC:** For example, scheduled drawdowns in water level within the unit

<sup>70</sup> **FWC:** If a unit is established as an ecotourism location, the quota is fixed and not adjusted further; Otherwise, the quota is adjusted based on the harvest data considerations described, above.

<sup>71</sup> **FWC:** These will only change if combined surveys of randomly selected water bodies show a significant increase or decline.

<sup>72</sup> **FWC:** Quota set at 2.4% of adult population size estimate when the unit was established; After 5-year reassessment survey conducted, the quota is either left unchanged or is reduced if there is reason for concern.

<sup>73</sup> **FWC:** Green zone = ± 25% of zone pre-harvest estimate; Yellow zone = decline < 50% of zone pre-harvest estimate; Red zone = decline ≥ 50% of zone pre-harvest estimate

<sup>74</sup> **FWC:** Aim to maintain population size within 25% of the pre-harvest estimate for each unit; Trends in population counts are monitored to determine whether changes in total abundance are occurring in the desired direction. The harvest quota in each variable quota unit is based on the estimated adult population size in the unit and decision thresholds correspond to action zones delineated relative to the estimated adult population size in the unit in 1988.

<sup>75</sup> **FWC:** Nine alternative statistical models (three linear, three non-linear in their treatment of year and water level covariate data, and three without a year effect) are fitted to population count data in each unit. The best model for each unit, each year, is selected based on Akaike Information Criterion (AIC) and is then used to estimate both the current and baseline (1988) population sizes, and to delineate decision action zones. Action zones then translate to different levels of allowable harvest in terms of the percentage of the adult alligator population in the unit that can be removed.

<sup>76</sup> **FWC:** 70% CI = 70% confidence interval around current estimate of the adult population size in a unit

<sup>77</sup> **FWC:** Quota = (estimated unit adult population size \* 0.06) / (mean proportion of unit quota taken) / (mean proportion of unit harvest consisting of adults)

<sup>78</sup> **FWC:** If this continues for 3 years, quota is set at 15% of the current estimate

<sup>79</sup> **FWC:** These quotas are not adjusted in relation to mean harvest proportions (i.e. unit quota and adult harvest); they are set at 12%, or 15%, of the estimated adult population

<sup>80</sup> **FWC:** Harvest closed regardless of the 70% CI

<sup>81</sup> **GADNR:** Reduce number of quota permits overall by 10% during regulation cycle, or reduce general quota permits while maintaining number of private lands permits

<b>Population monitoring data collected by agency<sup>83</sup></b>	Spotlight surveys: total counts, counts in 1ft. increment size classes, and counts in multiple unknown size classes; Associated covariates: temperature (air and water), water level, wave height, vegetation, moon phase and brightness, cloud cover	Spotlight surveys: total counts, counts in 2ft. increment size classes, and counts in multiple unknown size classes; Associated covariates: temperature (air and water), water level, water depth, wind velocity, % cloud cover; Nest counts <sup>84</sup>	Spotlight surveys <sup>85</sup> : total counts; Associated covariates: temperature (air and water), tide level, moon phase, wind velocity	Spotlight surveys: total counts, counts in <4ft. size class, counts in 2ft. increment size classes for alligators ≥4ft, and counts in unknown size class; Associated covariates: temperature (air and water), salinity, wind velocity
<b>Harvest data collected by agency</b>	Hunter harvest report form and annual survey <sup>86,87,88,89</sup> : Harvest date, county and location where taken <sup>90</sup> , carcass total length, sex, carcass disposition <sup>91</sup> , meat yield, processor information  Summarized data (by unit and statewide): Season length, bag limit, open zones, quota level, # permittees, total # alligators harvested, harvested alligators' lengths, weights, and sexes	Hunter harvest report form: Hunt dates and harvest date, method utilized, water body where taken <sup>92</sup> , carcass total length, weight, sex, # days hunted (effort); # of assistants  Summarized data (by zone and statewide): Season length, bag limit, open zones, quota level, # permittees, total # alligators harvested, harvested alligators' lengths, weights, and sexes	Check station data <sup>93</sup> (SW, WC) and self-report alligator harvest record sheet (SE): Harvest date, capture method, carcass total length, snout length, weight, sex, body girth, tail girth at base, location where taken <sup>94</sup> , # hours hunted (effort), # alligators observed during hunt, overall satisfaction with hunt; # of assistants  Summarized data (by zone): Season length, bag limit, open zones, quota level, # permittees, total # alligators harvested	Hunter harvest report form <sup>95,96</sup> : Whether or not permittee hunted, harvest date and time, harvest unit, county and location where taken <sup>97</sup> ; carcass length, weight, sex, total meat yield, hide disposition <sup>98</sup> , # hunting trips (effort), whether guide hired, method utilized <sup>99</sup>  Summarized data (by unit and statewide): Season length, bag limit, open zones, quota level, # permittees, total # alligators harvested, harvested alligators' lengths, weights, and sexes
<b>Other data for decision support collected by agency</b>	Nuisance data: # complaints received, # nuisance permits issued, # alligators taken <sup>100</sup> , complaint and removal	Nuisance data: # number complaints received, # nuisance permits issued, # alligators taken <sup>102</sup> , # man-	Nuisance data <sup>105</sup> : # nuisance permits issued, # alligators taken  Permit application data: #	Nuisance data: # number complaints received, # nuisance permits issued, # alligators taken <sup>106</sup> , whether

<sup>82</sup> **GADNR**: Increase number of quota permits overall by 10% during regulation cycle, or provide additional private lands permits

<sup>83</sup> Spotlight surveys provide basis for population size estimates and index values in each state

<sup>84</sup> **GADNR**: Nest surveys on Rhetts Island, which accounts for < 1% of the statewide population, are conducted along aerial transects by helicopter to provide reproductive index

<sup>85</sup> **ALDCNR**: ALDCNR is the only agency (of the four presented) that consistently conducts a single survey along each route each year (i.e. no replicates within year); Other states strive for at least two surveys per route each year, but are not always able to complete replicate surveys on all routes.

<sup>86</sup> **FWC**: Mailed to permittees along with permit, tags, and license.

<sup>87</sup> **FWC**: All permittees, including Statewide Trappers, Private Lands Trappers, and Nuisance Alligator Trappers complete harvest report forms, but annual surveys are only distributed to participants in the Statewide Alligator Harvest Program

<sup>88</sup> **FWC**: One harvest report form must be completed by each permittee for each CITES tag used; Report forms are submitted online or mailed, and they are not validated by FWC.

<sup>89</sup> **FWC**: For Nuisance Alligator Trappers, additional harvest report form data includes trapper permit information, area type or location, and for alligators <4ft relocated under a Special Purpose Permit, GPS capture and release locations

<sup>90</sup> **FWC**: Name of the lake or river, name of the harvest unit if taken in statewide harvest, or the property name if taken on private land

<sup>91</sup> **FWC**: Whether processed, discarded, or transferred

<sup>92</sup> **GADNR**: County and whether private or public water, and name of public water body if applicable

<sup>93</sup> **ALDCNR**: Collected when permittees bring harvested alligators to designated check station for validation and federal CITES tag (by posted station closing time on night/morning of hunt)

<sup>94</sup> **ALDCNR**: Name of river, creek, stream, or GPS coordinates

<sup>95</sup> **SCDNR**: Required from all permitted hunters (successful and unsuccessful), including those permitted for *WMA Alligator Hunt*; Forms are available online and can be submitted online or by email, fax, or mail. They must be completed within 24 hours and submitted within 5 days of harvest. Submitted data are not validated by SCDNR.

<sup>96</sup> **SCDNR**: For *WMA Alligator Hunt*, hunt parties are required to sign in and out of the WMA daily, and harvested alligators must be reported per permit specifications before the hunt party leaves the property.

<sup>97</sup> **SCDNR**: Location name, water body name, name of boat landing used, and GPS coordinates, if possible.

<sup>98</sup> **SCDNR**: Whether sold, kept, discarded, or given away

<sup>99</sup> **SCDNR**: First method used to gain control of alligator: hook and line, bow, crossbow, snare, harpoon, gig, or other

<sup>100</sup> **FWC**: Total and per complaint

	<p>locations, nuisance harvested alligator length</p> <p>Alligator bite database</p> <p>Permit application data: # quota permit applications (by applicant, statewide and by zone), applicant county of origin, applicant zone selections, application success/failure</p> <p>Statewide Alligator Harvest Program permitting process survey (2014)</p> <p>Experimental harvest data<sup>101</sup></p> <p>Growth rate data</p> <p>Nest survey data for Private Lands Alligator Management and Public Waters Alligator Egg and Hatchling Collection Programs</p>	<p>hours expended<sup>103</sup></p> <p>Permit application data: # quota permit applications (statewide and by zone), applicant county of origin, applicant priority points, applicant zone selections, application success/failure</p> <p>Hunter satisfaction surveys<sup>104</sup></p>	<p>quota permit applications, applicant county of origin, applicant priority points, applicant zone selections, application success/failure (statewide)</p>	<p>emergency or non-emergency scenario</p> <p>Permit application data: # quota permit applications (statewide and by unit), applicant county of origin, applicant priority points, applicant zone selections, application success/failure</p> <p>Mark-recapture data<sup>107</sup></p> <p>Water level data</p>
<p><b>Revenue and funding<sup>108</sup></b></p>	<p>FWC's Statewide Alligator Harvest Program (Private Lands Program, and Public Egg and Hatchling Program) is mostly self-sustaining, funded by revenue generated through license and tag fees</p> <p>Revenue from fees goes into the State Game Trust Fund, then is allocated by the state legislature back to FWC to fund a variety of programs</p>	<p>GADNR's alligator harvest program is funded by the Wildlife Resources Division Game Management Section's regular operating funds; No additional funding for monitoring or harvest program administration is generated by license fees</p> <p>Any revenue generated through license sales is allocated by the state legislature to GADNR, but not back specifically to the Wildlife Resources Division</p>	<p>ALDCNR's alligator harvest program<sup>109</sup> is funded by the agency's regular operating funds; No additional funding for monitoring or harvest program administration is generated by license or permit application fees</p> <p>Revenue generated through license sales and permit application fees goes into the state Game and Fish Fund for the ALDCNR Wildlife and Freshwater Fisheries Division Wildlife Section, but it does not go back specifically to the alligator program<sup>110</sup></p>	<p>SCDNR's alligator harvest program, including research and management activities, is funded (by legal mandate) by the revenue generated by application fees, permit sales and tag fees (but not license fees; however, alligator management program personnel are funded by SCDNR Wildlife Management Section regular operating funds</p>

<sup>102</sup> **FWC:** Total and per complaint

<sup>105</sup> **ALDCNR:** Some information about the number and type of complaints is collected at the district level

<sup>106</sup> **FWC:** Total and per complaint

<sup>101</sup> **FWC:** Includes mark-recapture, mark-resight, mark-recovery, nesting effort, survivorship of nests, # eggs in nests, # hatchlings produced

<sup>103</sup> **GADNR:** Total and per complaint

<sup>104</sup> **GADNR:** Distributed to unsuccessful permittees in 2003 and 2008; Distributed to 50% of permittees in 2013

<sup>107</sup> **SCDNR:** Marking completed by SCDNR, but little effort expended towards recapture thus far

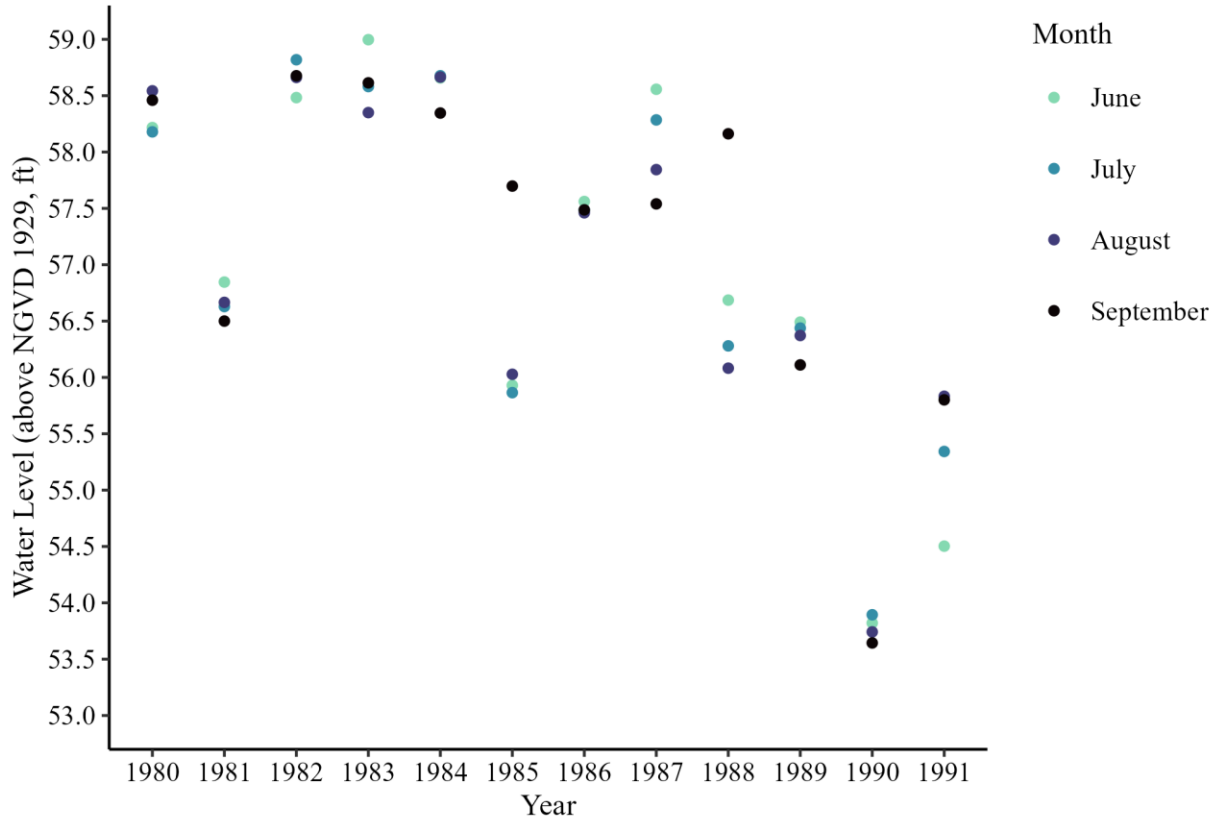
<sup>108</sup> None of the agencies are able to use Pittman-Robertson funds for alligator population monitoring and management because alligators are reptiles (not a traditional "fur or feathers" game species).

<sup>109</sup> **ALDCNR:** The agency considers their alligator harvest program to be an alligator hunt, rather than a formal "program".

<sup>110</sup> **ALDCNR:** These funds are more likely directed towards monitoring and management of other game species, such as deer.

## Appendix B

### Orange Lake Monthly Mean Water Level (1980 – 1991)



Real OL water level data, monthly means for summer months. Mean and SD of these data were used to simulate WL co-variate data for the first replicate ( $j = 1$ ) count survey each year ( $t$ ) (U.S. Geological Survey, 2016).

U.S. Geological Survey. (2016). *National Water Information System data available on the World Wide Web*. USGS Water Data for the Nation. <https://doi.org/10.5066/F7P55KJN>, accessed 09/17/2020, at URL [https://waterdata.usgs.gov/nwis/inventory/?site\\_no=02242450&agency\\_cd=USG](https://waterdata.usgs.gov/nwis/inventory/?site_no=02242450&agency_cd=USG)

## Appendix C

### R Code for Alligator Population Simulation Model

```
## Appendix C. R code for alligator population simulation model
rm(list = ls())

## Load packages
library(tibble)
library(tidyr)
library(purrr) # for map_invoke and other map fxns
library(msm) # for truncated normal distribution (msm::rtnorm)
library(dplyr, warn.conflicts = FALSE) # for mutate
library(plyr)
library(data.table) # *** ?getDThreads #setDTthreads(1)

## Specify date for file names of objects saved
thedata <- strftime(Sys.Date(), "%y%m%d")

## Set working directory when working on personal HP laptop
setwd("C:/Users/tbeja/OneDrive - University of Georgia/Dissertation/OrangeLakeIPM")

## Define function to sim timeseries to make rep IPM datasets from
programs/m_simRepPops.R (10/21/22)]-----
sim_pop_221021 <-
  function(x = NULL,
           lamda = NULL,
           fileID = thedate,
           return_pop = NULL,
           save_pop = NULL,
           saverDS_gators = NULL,
           saverDS_repro = NULL,
           pop = NULL,
           gators = NULL,
           start_t,
           end_t,
           tH0,
           n_reps,
           n_years,
           detectProb = 1,
           successRate = 1,
           ...) {
    set.seed(110122)
    phi0 = c(0.41, 0.843, 0.8552, 0.9057, 0.823) # baseline annual survival probs
    b_k = c(-1.4272, -2.0244, -4.129, -11.715, -3.264) # slopes for DD survival
    b_D = 39.622 # slope for DD puberty
    adD_0 = 0.193 # baseline adult density for DD survival and puberty

    # Define size classes based on total length (TL cm)
    size_class <-
      cut(
        c(1:500),
```

```

    breaks = c(-Inf, 30, 122, 183, 274, Inf),
    right = FALSE,
    include.lowest = FALSE,
    labels = c(1:5)
  )

# Latent states; 5 size classes(1:5) + three harvest classes(6:8) + dead(9)
state <- factor(1:9, labels = c(levels(size_class), c(6:9)))

# Area of Orange Lake
OL.ha <- 5251.5 # hectares

# Clarify harvest policy to apply during hunting season:
# - defaults to 0, lamda is constant rate, x[1:3] = f(alpha,beta,Qmax)
if (!missing(x)) {
  harvest_policy <- c(round(x[1], 5), round(x[2], 1), round(x[3], 1))
}
if (!missing(lamda)) {
  harvest_policy <- lamda
}
if (missing(x) & missing(lamda)) {
  harvest_policy <- 0
}

# Specify whether annual nesting and individual alligator records kept
if (!missing(saveRDS_gators)) {
  save_gators <- TRUE
} else {
  save_gators <- FALSE
}
if (!missing(saveRDS_repro)) {
  save_repro <- TRUE
} else {
  save_repro <- FALSE
}

#[FUNCTION: Size-specific sex assignment]
assign_sex <- function(n, sex_ratio) {
  sex <- rbinom(as.numeric(n), 1, sex_ratio) + 1 # 1=female, 2=male
  return(sex)
}

#[FUNCTIONs: Convert SVL to TL or vice versa based on sex-specific conversion]
make_TL <- function(size, sex) {
  a_svlTL <- c(2.2390, 2.3121)
  b_svlTL <- c(0.9707, 0.9622)
  TL <- a_svlTL[sex] * (size ^ b_svlTL[sex])
  return(TL)
}
make_SVL <- function(size, sex) {
  # a & b parameter values from Table 7 Woodward et al. 1992; c(F,M)
  a_svlTL <- c(2.2390, 2.3121)
  b_svlTL <- c(0.9707, 0.9622)

```

```

SVL <- (size / a_svlTL[sex]) ^ (1 / b_svlTL[sex])
return(SVL)
}

#[FUNCTION: Alligator growth model, Baker-form of Schnute model]
grow <- function(sex, Ym) {
  tau = c(0, 45) # age (yrs) at hatchling and max life expectancy
  deltaT = 1 # duration of growth period
  y1 = 12.5 # SVL at hatching (cm)
  y2 = c(135.9, 186.9) # terminal SVL c(F,M)
  a = c(0.11, 0.09)
  b = c(0.72, 0.69) # growth rate(a) and shape(b) c(F,M)
  modelErr = c(5.9, 7.42) # model error c(F,M)

  # Compute expected SVL after annual growth, use to draw realized value from
  # normal distribution, then convert to TL if below terminal size for sex;
  # otherwise, keep last TL
  iYr <- (((Ym ^ b[sex]) * exp(-a[sex] * deltaT)) +
           ((y2[sex] ^ b[sex]) - (y1 ^ b[sex]) * exp(-a[sex] * (tau[2] -
tau[1])))) *
           (((1 - exp(-a[sex] * deltaT)) /
            (1 - exp(
              -a[sex] * (tau[2] - tau[1])
            )))) ^ (1 / b[sex]) %>%
           rtnorm(
             n = length(.),
             mean = .,
             sd = sqrt(modelErr[sex]),
             lower = Ym
           )
  newTL <- ifelse(Ym <= y2[sex],
                 make_TL(size = iYr, sex = sex),
                 make_TL(size = Ym, sex = sex))

  return(round(as.numeric(newTL), 1)) # TL(cm) for t+1
}

#[FUNCTION: ...]
set_quota <-
function(harvest_policy,
        Nh_t,
        detectProb,
        successRate) {
  # Harvestable pop count (imperfect detection of Nh_t for state-dep. policy)
  yNh_t <- rbinom(n_reps, Nh_t, detectProb)

  if (length(harvest_policy) > 1) {
    eta <- 1 / (1 + exp(harvest_policy[1] * (harvest_policy[2] - yNh_t)))
    Q <- round(eta * harvest_policy[3]) # harvest quota
    H <- rbinom(n_reps, Q, successRate)
  } else {
    H <- rbinom(n_reps, yNh_t, harvest_policy * successRate)
  }
}

```

```

    return(H) # total harvest
  }

dd) #'#[FUNCTION: annual survival outside harvest for each i based on z and t(due to
get_phi_it <- function(phi_ct, z_it) {
  phi_it <- phi_ct[as.integer(z_it)]
  return(phi_it)
}

#' [FUNCTION: Probability that adult female reaches sexual maturity given TL]
# her_TL=180.5; adult_density=0.193
puberty <- function(her_TL, adD_t = NULL) {
  base_offset <-
    -(-17.46644 / 0.087134877) # baseline TL offset for OL (200.4529)
  OL_slope <- 0.087134877 # slope logit(pM) by female TL

  if (is.null(adD_t)) {
    logit_pM <- OL_slope * (her_TL - base_offset)
  } else {
    DD_offset <- base_offset + (b_D * (log10(adD_t) - log10(adD_0)))
    logit_pM <- OL_slope * (her_TL - DD_offset)
  }
  pM <- 1 / (1 + exp(-(logit_pM))) # convert to probability scale

  sexually_mature <- rbinom(length(pM), 1, prob = pM)
  return(sexually_mature)
}

#' [FUNCTION: ...]
nesting <- function(N_adFM, save_repro, mean_clutch = 33) {
  repro <- imap_dfr(N_adFM, ~ {
    nests <- rbinom(.x, 1, prob = 0.398)
    surviving_nests <- rbinom(nests, 1, prob = 0.452) * nests
    eggs <- rpois(.x, mean_clutch) * surviving_nests
    surviving_eggs <- rbinom(length(eggs), eggs, prob = 0.875)
    repro <- data.table(nests,
                        surviving_nests,
                        eggs,
                        surviving_eggs,
                        rep = .y,
                        year = t)
  })
  if (save_repro == TRUE) {
    if (t == 1) {
      saveRDS(repro, file = paste0("data/raw_data/repro_", fileID, ".RDS"))
    } else {
      old <- readRDS(file = paste0("data/raw_data/repro_", fileID, ".RDS"))
      data <- repro
      updated <- bind_rows(old, data)
      saveRDS(updated,
               file = paste0("data/raw_data/repro_", fileID, ".RDS"))
    }
  }
}

```

```

    }
    return(repro$surviving_eggs)
  }

#[FUNCTION: make new hatchlings to add to survivors of t, in t+1]
recruitment <-
  function(n_recruits,
           last_id,
           year_hatched,
           pop_rep) {
    #'[FUNCTION: for ...]
    f_hatch_TL <- function(n_hatched, sex) {
      svl <- runif(n_hatched,
                  min = make_SVL(18, sex),
                  max = make_SVL(30, sex))
      hatchling_TLs <- make_TL(size = svl,
                               sex = sex)

      return(hatchling_TLs)
    }
    recruits <- tibble(
      sex = as.integer(assign_sex(n = n_recruits,
                                  sex_ratio = 0.5)),
      TL = as.double(f_hatch_TL(
        n_hatched = n_recruits,
        sex = sex
      )),
      z = factor(as.integer(size_class[TL]), levels = 1:9),
      t_recruit = rep(as.integer(year_hatched + 1),
                      length = n_recruits),
      mature = if_else(sex == as.integer(1), as.integer(0),
                       as.integer(NA)),
      f = as.integer(NA),
      rep = pop_rep
    ) %>%
      arrange(., desc(z), sex, desc(TL)) %>%
      add_column(.,
                 ind = as.character((last_id + 1):(last_id + n_recruits)),
                 .before = 1) %>%
      setDT(.)
    return(recruits)
  }

#[FUNCTION: ...]
save_i_data <- function(data, year) {
  if (year == 1) {
    saveRDS(data,
             file = paste0("data/raw_data/gators_summ_", fileID, ".RDS"))
  } else {
    old <-
      readRDS(file = paste0("data/raw_data/gators_summ_", fileID, ".RDS"))
    updated <- bind_rows(old, data)
    saveRDS(updated,
             file = paste0("data/raw_data/gators_summ_", fileID, ".RDS"))
  }
}

```

```

}
}

#[FUNCTION: Based on i records for year t, generate i records object for t+1]
year_end <- function(gators_t) {
  # Remove gators that were dead at the beginning of t
  gators_t1 <- gators_t[z != "9",]

  # Convert state z from factor to integer for ease in next steps
  gators_t1[, z := as.integer(z)]

  # Harvest recoveries at the beginning of t now dead (for t+1)
  gators_t1[z %in% 6:8, z := 9]

  # Update records for harvested gators
  gators_t1[h == 1, ':= ' (z = z + 3, TL = 0, f = 0)]

  # Update state for gators that died of non-harvest mortality in t
  gators_t1[which(z <= 5 &
                 h == 0 & s == 0), ':= ' (z = 9, TL = 0, f = 0)]

  # Grow surviving individuals
  gators_t1[s == 1, TL := grow(sex = gators_t1[s == 1, sex],
                              Ym = make_SVL(size = gators_t1[s == 1, TL],
                                             sex = gators_t1[s == 1, sex]))]

  # Update state for survivors
  gators_t1[s == 1, z := as.integer(size_class[gators_t1[s == 1, TL]])]
  gators_t1[, z := factor(z, levels = state)]

  # Reset fecundity
  gators_t1[, f := as.integer(NA)]

  Nrecruits <-
    gators_t[, sum(f, na.rm = TRUE), by = rep] %>% pull(V1)

  pop_t1 <- imap(Nrecruits, function(n, r) {
    if (n == 0) {
      gators_t1[rep == r,
                c("rep",
                  "ind",
                  "sex",
                  "TL",
                  "z",
                  "t_recruit",
                  "mature",
                  "f")]
    } else {
      bind_rows(
        gators_t1[rep == r,
                  c("rep",
                    "ind",
                    "sex",

```

```

        "TL",
        "Z",
        "t_recruit",
        "mature",
        "f")],
    recruitment(
      n_recruits = n,
      last_id = max(as.integer(gators_t[rep == r, ind])),
      year_hatched = t,
      pop_rep = r
    )
  )
}
}) %>% rbindlist()

next_gators <-
  bind_cols(
    pop_t1,
    t_obs = rep(as.numeric(NA), nrow(pop_t1)),
    h = rep(as.numeric(NA), nrow(pop_t1)),
    phi_it = rep(as.numeric(NA), nrow(pop_t1)),
    s = rep(as.integer(NA), nrow(pop_t1))
  )
return(next_gators)
}

make_founders <- function(N0_k) {
  set.seed(2021)

  size_lims <- c(18, 30, 122, 183, 274, 300) # TL cm
  svl_lims <- array(
    c(
      size_lims[1:5] %>% make_SVL(size = ., sex = 1),
      size_lims[2:6] %>% make_SVL(size = ., sex = 1),
      size_lims[1:5] %>% make_SVL(size = ., sex = 2),
      size_lims[2:6] %>% make_SVL(size = ., sex = 2)
    ),
    dim = c(5, 2, 2),
    dimnames = list(c(), c("min", "max"), c("F", "M"))
  )
  # Draw sex variable for each founding population member
  p_male <-
    c(0.5, 0.63, 0.53, 0.53, 0.90) # size class-specific ratio M to F

  pop <- map_df(as.integer(unique(size_class)),
    function(c)
      tibble(
        size_class = rep(c, N0_k[c]),
        sex = assign_sex(n = N0_k[c],
          sex_ratio = p_male[c]) %>%
          as.integer
        ) %>%

```

```

    mutate(mature = if_else(.$sex == 1, as.integer(0), as.integer(NA))) %>%
    arrange(., sex) %>% mutate(TL = 0) %>% setDT(.)
pop[, TL := map2_dbl(
  pop$sex,
  pop$size_class,
  ~ runif(1, min = svl_lims[.y, "min", .x],
    max = svl_lims[.y, "max", .x]) %>%
    make_TL(size = ., sex = .x)
)]
pop[, z := state[pop$size_class]]
setorder(pop, -z, -TL, -sex, na.last = TRUE)
pop[, t_recruit := 1][, f := as.numeric(NA)]
setorder(pop, -z, sex, -TL)
pop[, ind := as.character(1:sum(N0_k))]
return(pop)
}

gators <- replicate(n = n_reps,
  expr = make_founders(N0_k = c(685, 4100, 950, 1080, 720)),
  simplify = FALSE) %>%
  rbindlist(., idcol = "rep")

# Array for annual state-specific records
pop <- array(
  as.numeric(NA),
  dim = c(9, n_years, 5, n_reps),
  dimnames = list(
    state = NULL,
    year = NULL,
    data = c("N", "H", "phi", "M", "S"),
    rep = seq(n_reps)
  )
)

## Loop through years
for (t in start_t:end_t) {
  ## [FALL CENSUS] ----
  pop[, t, "N", ] <-
    gators[!is.na(z), summary(z, .drop = FALSE), by = rep] %>%
    pull(V1) %>% matrix(., nrow = 9, byrow = FALSE)

  gators[!is.na(z), "t_obs" := t][!is.na(z), "h" := 0]

  ## [HARVEST] ----
  if (t < tH0 | sum(harvest_policy) == 0) {
    pop[, t, "H", ] <- 0
  } else {
    # Take number of sa+, get expected take, realize take per hunter success rate
    pop[3:5, t, "N", ] %>% colSums() %>% as.numeric() %>%
      set_quota(
        harvest_policy,
        Nh_t = .,

```

```

    detectProb = detectProb,
    successRate = successRate
  ) %>%
  imap(., ~ {
    sample(x = gators[z %in% c(3:5) & rep == .y, ind],

           size = min(sum(pop[3:5, t, "N", .y]), .x),
           replace = FALSE)

  }) %>%
  imap(., ~ {
    gators[!is.na(z) & rep == .y & ind %in% .x, h := 1]
  }) %>% rbindlist
# If gators taken
if (any(gators$h == 1, na.rm = FALSE)) {
  # Record number harvested by size class
  pop[, t, "H",] <- gators[!is.na(z) & h == 1,
                          summary(z, .drop = FALSE), by = rep] %>%
    pull(V1) %>%
    matrix(.,
           ncol = n_reps,
           nrow = 9,
           byrow = FALSE) # added 10/10/2022

} else {
  pop[, t, "H",] <- 0
}
}

# Post-harvest adult density
adD_t <- map_dbl(seq(n_reps),
                ~ pop[4:5, t, c("H", "N"), .x] %>%
                  colSums %>% diff %>% as.numeric(.) / OL.ha)
## Compute density-dependent survival rates for remainder of the year
pop[, t, "phi",] <-
  #dd_phi(adD_0 = adD_0, b_c = b_k, phi0 = phi0, D_t = adD_t)
  suppressMessages(map_dfc(
    adD_t,
    ~
    plogis(q = qlogis(phi0) +
           (b_k * (
             log10(.x) - log10(adD_0)
           ))) %>%
    round(digits = 4) %>%
    c(., 0, 0, 0, 0)
  ) %>%
  as.matrix() %>% unname)
gators[!is.na(z),
  phi_it := map2_dbl(as.integer(gators[!is.na(z), z]),
                    as.integer(gators[!is.na(z), rep]),
                    ~ {
                      get_phi_it(phi_ct = pop[, t, "phi", .y], z_it = .x)
                    }
  )][!is.na(z) & h == 1, phi_it := 0][!is.na(z) &

```

```

as.integer(z)
<= 5 & h == 0 & (t - t_recruit > 40),
max(0.01, 0.60 - 0.59 * (((t - t_recruit) - 40) / (75 - 40))), by = "ind"[!is.na(z),
s := rbinom(n = nrow(gators[!is.na(z), ]),
size = 1,
prob = gators[!is.na(z), phi_it])]

# Mortality count; no. alive at beg. of t, not harvested, but died
pop[, t, "M",] <-
  gators[!is.na(z), summary(z[TL != 0 & h == 0 & s == 0],
    .drop = FALSE), by = rep] %>%
  pull(V1) %>%
  matrix(.,
    ncol = n_reps,
    nrow = 9,
    byrow = FALSE) # added 10/10/2022

pop[, t, "S",] <-
  pop[, t, "N",] - pop[, t, "H",] - pop[, t, "M",]

## [PUBERTY] ----
gators[!is.na(z) & TL >= 183 & sex == 1 & s == 1 & mature == 0,
  mature :=
  puberty(her_TL = gators[!is.na(z), TL[.I[TL >= 183 &
    sex == 1 & s == 1 & mature
== 0]]],
  add_t = add_t[as.integer(gators[!is.na(z), rep[.I[TL >= 183 &
    sex == 1 &
s == 1 &
mature ==
0]]))]]]

## [NESTING] ----
gators[!is.na(z) & s == 1 & mature == 1,
  f := nesting(N_adFM = gators[!is.na(z) &
    s == 1 & mature == 1, .N, by = rep]$N,
  save_repro = save_repro)]

if (save_gators == TRUE) {
  save_i_data(data = gators[!is.na(z), ], year = t)
}
## [RECRUITMENT & GROWTH] ----
# Update pop records for t+1 and integrate records for new recruits w/
# existing population members
if (t < n_years) {
  gators <- year_end(gators_t = gators[!is.na(z),])
}
} # close t loop

```

```

# Save replicate population timeseries records
if (!missing(save_pop)) {
  saveRDS(pop, file = paste0("data/raw_data/pop_ts_", fileID, ".RDS"))
}

if (!missing(return_pop)) {
  utility_ts <- list(U = utility, pop = pop)
  return(utility_ts)
} else {
  return(pop)
}

} # close sim_pop

## Simulate timeseries with constant harvest rate (0.13) -----
lamda_ts <-
sim_pop_221021(
  lamda = 0.13,
  fileID = paste0("_lamda_", thedate),
  return_pop = TRUE,
  save_pop = TRUE,
  saveRDS_gators = TRUE,
  saveRDS_repro = TRUE,
  successRate = 0.875,
  n_reps = 10,
  th0 = 51,
  n_years = 62,
  start_t = 1,
  end_t = 62
) # fitness = 3.43

#####
set.seed(110122)
#' [FUNCTION: Simulate population timeseries for years before harvest (1:(th0-1))
#' and save gators and pop objects; then, run sim_pop_from_th0]
sim_pop_before_th0 <- function(n_reps = 20,
                              n_years = 181,
                              th0 = 81,
                              save_gators = FALSE,
                              save_repro = FALSE,
                              phi0 = c(0.41, 0.843, 0.8552, 0.9057, 0.823),
                              b_k = c(-1.4272, -2.0244, -4.129, -11.715, -3.264),
                              b_D = 39.622,
                              adD_0 = 0.193) {
  # Define size classes based on total length (TL cm)
  size_class <-
  cut(
    c(1:500),
    breaks = c(-Inf, 30, 122, 183, 274, Inf),
    right = FALSE,
    include.lowest = FALSE,
    labels = c(1:5)

```

```

)

# Latent states; 5 size classes(1:5) + three harvest classes(6:8) + dead(9)
state <- factor(1:9, labels = c(levels(size_class), c(6:9)))

#' Area of Orange Lake
OL.ha <- 5251.5 # hectares

#'[FUNCTION: Size-specific sex assignment]
assign_sex <- function(n, sex_ratio) {
  sex <- rbinom(as.numeric(n), 1, sex_ratio) + 1 # 1=female, 2=male
  return(sex)
}

#'[FUNCTIONs: Convert SVL to TL or vice versa based on sex-specific conversion]
make_TL <- function(size, sex) {
  a_svlTL <- c(2.2390, 2.3121)
  b_svlTL <- c(0.9707, 0.9622)
  TL <- a_svlTL[sex] * (size ^ b_svlTL[sex])
  return(TL)
}
make_SVL <- function(size, sex) {
  # a & b parameter values from Table 7 Woodward et al. 1992; c(F,M)
  a_svlTL <- c(2.2390, 2.3121)
  b_svlTL <- c(0.9707, 0.9622)
  SVL <- (size / a_svlTL[sex]) ^ (1 / b_svlTL[sex])
  return(SVL)
}

#'[FUNCTION: Alligator growth model, Baker-form of Schnute model]
grow <- function(sex, Ym) {
  tau = c(0, 45) # age (yrs) at hatchling and max life expectancy
  deltaT = 1 # duration of growth period
  y1 = 12.5 # SVL at hatching (cm)
  y2 = c(135.9, 186.9) # terminal SVL c(F,M)
  a = c(0.11, 0.09)
  b = c(0.72, 0.69) # growth rate(a) and shape(b) c(F,M)
  modelErr = c(5.9, 7.42) # model error c(F,M)

  # Compute expected SVL after annual growth, use to draw realized value from
  # normal distribution, then convert to TL if below terminal size for sex;
  # otherwise, keep last TL
  iYr <- (((Ym ^ b[sex]) * exp(-a[sex] * deltaT)) +
    ((y2[sex] ^ b[sex]) - (y1 ^ b[sex]) * exp(-a[sex]*(tau[2] - tau[1])))) *
    ((1 - exp(-a[sex] * deltaT)) /
      (1 - exp(
        -a[sex] * (tau[2] - tau[1])
      )))) ^ (1 / b[sex]) %>%
  rtnorm(
    n = length(.),
    mean = .,
    sd = sqrt(modelErr[sex]),
    lower = Ym
  )
}

```

```

)
newTL <- ifelse(Ym <= y2[sex],
               make_TL(size = iYr, sex = sex),
               make_TL(size = Ym, sex = sex))

return(round(as.numeric(newTL), 1)) # TL(cm) for t+1
}

#[FUNCTION: Create initial population, no replicates]
make_founders <- function(N0_k) {
  set.seed(2021)

  # Draw sex variable for each founding population member
  p_male <-
    c(0.5, 0.63, 0.53, 0.53, 0.90) # size class-specific ratio M to F

  pop <- map(as.integer(unique(size_class)),
            function(c)
              tibble(
                size_class = rep(c, N0_k[c]),
                sex = assign_sex(n = N0_k[c],
                                sex_ratio = p_male[c]) %>%
                  as.integer
              ) %>%
              arrange(., sex) %>% mutate(TL = 0))

  size_lims <- c(18, 30, 122, 183, 274, 300)

  svl_lims <-
    array(
      c(
        size_lims[1:5] %>% make_SVL(size = ., sex = 1),
        size_lims[2:6] %>% make_SVL(size = ., sex = 1),
        size_lims[1:5] %>% make_SVL(size = ., sex = 2),
        size_lims[2:6] %>% make_SVL(size = ., sex = 2)
      ),
      dim = c(5, 2, 2),
      dimnames = list(c(), c("min", "max"), c("F", "M"))
    )

  pop <- map_dfr(seq(pop), function(c)
    pop[[c]] %>% setDT(.))

  pop[, TL := map2_dbl(
    pop$sex,
    pop$size_class,
    ~ runif(1, min = svl_lims[.y, "min", .x],
            max = svl_lims[.y, "max", .x]) %>%
      make_TL(size = ., sex = .x)
  )]

  founders <- tibble(sex = pop$sex, TL = pop$TL) %>%
    mutate(z = size_class[TL] %>% factor(., levels = state)) %>%

```

```

    arrange(., desc(z), sex, desc(TL)) %>%
    mutate(t_recruit = as.integer(1), .before = 4) %>%
    mutate(mature = if_else(sex == as.integer(1),
                           as.integer(0),
                           as.integer(NA))) %>%
    mutate(f = as.integer(NA)) %>%
    mutate(ind = as.character(1:sum(N0_k)), .before = 1) %>% setDT
  return(founders)
}

#[FUNCTION: ...]
list2cols <- function(x) {
  x %>% unlist %>%
  matrix(., nrow = n_reps, byrow = TRUE) %>% t()
}

#[FUNCTION: compute density-dependent size-specific annual survival]
dd_phi <- function(adD_0, b_c, phi0, D_t) {
  suppressMessages(map_dfc(D_t, ~
    plogis(q = qlogis(phi0) + (
      b_c * (log10(.x) - log10(adD_0))
    )) %>%
    round(digits = 4) %>%
    c(., rep(0, 4))) %>% as.matrix() %>% unname) }

###[FUNCTION: nnuual survival outside harvest for each i based on z and t(due to dd)
get_phi_it <- function(phi_ct, z_it) {
  phi_it <- phi_ct[as.integer(z_it)]
  return(phi_it)
}

#[FUNCTION: Probability that adult female reaches sexual maturity given TL]
# her_TL=180.5; adult_density=0.193
puberty <- function(her_TL, adD_t = NULL) {
  base_offset <-
    -(-17.46644 / 0.087134877) # baseline TL offset for OL (200.4529)
  OL_slope <-
    0.087134877 # slope logit(pM) by female TL

  if (is.null(adD_t)) {
    logit_pM <- OL_slope * (her_TL - base_offset)
  } else {
    DD_offset <- base_offset + (b_D * (log10(adD_t) - log10(adD_0)))
    logit_pM <- OL_slope * (her_TL - DD_offset)
  }
  pM <- 1 / (1 + exp(-logit_pM)) # convert to probability scale
  sexually_mature <- rbinom(length(pM), 1, prob = pM)
  return(sexually_mature)
}

#[FUNCTION: ...]
nesting <- function(N_adFM, save_repro) {
  mean_clutch = 33

```

```

repro <- imap_dfr(N_adFM, ~ {
  nests <- rbinom(.x, 1, prob = 0.398)
  surviving_nests <- rbinom(nests, 1, prob = 0.452) * nests
  eggs <- rpois(.x, mean_clutch) * surviving_nests
  surviving_eggs <- rbinom(length(eggs), eggs, prob = 0.875)
  repro <- data.table(nests,
                     surviving_nests,
                     eggs,
                     surviving_eggs,
                     rep = .y,
                     year = t)
})
if (save_repro == TRUE & t >= (tH0 - 1)) {
  if (t == (tH0 - 1)) {
    saveRDS(repro, file = "repro_040422.RDS")
  } else {
    old <- readRDS(file = "repro_040422.RDS")
    data <- repro
    updated <- bind_rows(old, data)
    saveRDS(updated, file = "repro_040422.RDS")
  }
}
return(repro$surviving_eggs)
}

#[FUNCTION: make table for new hatch to add to survivors of t, in t+1]
recruitment <-
function(n_recruits,
        last_id,
        year_hatched,
        pop_rep) {
  #[FUNCTION: for ...]
  f_hatch_TL <- function(n_hatched, sex) {
    svl <- runif(n_hatched,
                min = make_SVL(18, sex),
                max = make_SVL(30, sex))
    hatchling_TLs <- make_TL(size = svl,
                             sex = sex)
    return(hatchling_TLs)
  }
  recruits <- tibble(
    sex = as.integer(assign_sex(n = n_recruits,
                               sex_ratio = 0.5)),
    TL = as.double(f_hatch_TL(
      n_hatched = n_recruits,
      sex = sex
    )),
    z = factor(as.integer(size_class[TL]), levels = 1:9),
    t_recruit = rep(as.integer(year_hatched + 1),
                    length = n_recruits),
    mature = if_else(sex == as.integer(1), as.integer(0),
                     as.integer(NA)),
    f = as.integer(NA),

```

```

    rep = pop_rep
  ) %>% #factor(pop_rep, levels = seq(n_reps))
  arrange(., desc(z), sex, desc(TL)) %>%
  add_column(.,
             ind = as.character((last_id + 1):(last_id + n_recruits)),
             .before = 1) %>%
  setDT(.)
  return(recruits)
}

#[FUNCTION: ...]
save_i_data <- function(data, year) {
  if (year == (tH0 - 1)) {
    saveRDS(data, file = paste0("gators_summ_", thedate, ".RDS"))
  } else {
    old <- readRDS(file = paste0("gators_summ_", thedate, ".RDS"))
    updated <- bind_rows(old, data)
    saveRDS(updated, file = paste0("gators_summ_", thedate, ".RDS"))
  }
}

#[FUNCTION: Based on i records for year t, generate i records object for t+1]
year_end <- function(gators_t) {
  # Remove gators that were dead at the beginning of t
  gators_t1 <- gators_t[z != "9",]

  # Convert state z from factor to integer for ease in next steps
  gators_t1[, z := as.integer(z)]

  # Harvest recoveries at the beginning of t now dead (for t+1)
  gators_t1[z %in% 6:8, z := 9]

  # Update records for harvested gators
  gators_t1[h == 1, ':= ' (z = z + 3, TL = 0, f = 0)]

  # Update state for gators that died of non-harvest mortality in t
  gators_t1[which(z <= 5 &
                 h == 0 & s == 0), ':= ' (z = 9, TL = 0, f = 0)]

  # Grow surviving individuals
  gators_t1[s == 1, TL := grow(sex = gators_t1[s == 1, sex],
                              Ym = make_SVL(size = gators_t1[s == 1, TL],
                                             sex = gators_t1[s == 1, sex]))]

  # Update state for survivors
  gators_t1[s == 1, z := as.integer(size_class[gators_t1[s == 1, TL]])]
  gators_t1[, z := factor(z, levels = state)]

  # Reset fecundity
  gators_t1$f <- as.integer(NA)

  # Updated records for t+1
  updated_gators <-

```

```

gators_t1[, c("ind", "sex", "TL", "z", "t_recruit",
             "mature", "f", "rep")]

pop_t1 <-
gators_t[, sum(f, na.rm = TRUE), by = rep] %>% pull(V1) %>%
imap(., function(n, r) {
  if (n == 0) {
    updated_gators[rep == r,]
  } else {
    recruitment(
      n_recruits = n,
      last_id = max(as.integer(gators_t[rep == r, ind])),
      year_hatched = t,
      pop_rep = r
    ) %>%
      bind_rows(updated_gators[rep == r,], .)
  }
}) %>% rbindlist()
return(pop_t1)
}

#' Create array for annual state-specific records
pop <- array(
  as.numeric(NA),
  dim = c(9, n_years, 5, n_reps),
  dimnames = list(
    state = NULL,
    year = NULL,
    data = c("N", "H", "phi", "M", "S"),
    rep = seq(n_reps)
  )
)

gators <- replicate(n = n_reps,
                    expr = make_founders(N0_k = c(685, 4100, 950, 1080, 720)),
                    simplify = FALSE) %>% rbindlist(., idcol = "rep")

for (t in 1:(tH0 - 1)) {
  ## [FALL CENSUS] ----
  pop[, t, "N",] <-
  gators[, summary(z, .drop = FALSE), by = rep] %>%
  pull(V1) %>% list2cols()

  gators[, "t_obs" := t][, "h" := 0] # add column for year variable

  ## [HARVEST] ----
  pop[, t, "H",] <- 0

  # Post-harvest adult density
  adD_t <- map_dbl(seq(n_reps), ~ {
    pop[4:5, t, c("H", "N"), .x] %>% colSums %>% diff %>%
    as.integer(.) / OL.ha
  })
}

```

```

#any(adD_t == 0) {break}

## [SURVIVAL] ----
## Compute density-dependent survival rates for remaining of the year
pop[, t, "phi",] <-
  dd_phi(
    adD_0 = adD_0,
    b_c = b_k,
    phi0 = phi0,
    D_t = adD_t
  )

gators[, phi_it := map2_dbl(as.integer(gators$z), as.integer(gators$rep),
  ~ {
    get_phi_it(phi_ct = pop[, t, "phi", .y], z_it = .x)
  }][h == 1, phi_it := 0][as.integer(z) <= 5 &
  h == 0 & (t - t_recruit >
40),
  phi_it := max(0.01, 0.60 -
0.59 * (((t - t_recruit) - 40) / (75 -
40))), by = "ind"][, s := rbinom(n = nrow(gators),
size = 1,
prob = gators$phi_it)]

# Mortality count; no. alive at beg. of t, not harvested, but died
pop[, t, "M",] <-
  gators[, summary(z[TL != 0 & h == 0 & s == 0],
    .drop = FALSE), by = rep] %>%
  pull(V1) %>% list2cols()

pop[, t, "S",] <-
  pop[, t, "N",] - pop[, t, "H",] - pop[, t, "M",]

#pop[, t, c("N","H","M), ] %>% diff

## [PUBERTY] ----
gators[TL >= 183 & sex == 1 & s == 1 & mature == 0, mature :=
  puberty(her_TL = gators[, TL[.I[TL >= 183 &
    sex == 1 & s == 1 & mature == 0]]],
  adD_t = adD_t[as.integer(gators[, rep[.I[TL >= 183 &
    sex == 1 & s == 1 &
mature == 0]])]))]

## [NESTING] ----
gators[s == 1 & mature == 1,
  f := nesting(N_adFM = gators[s == 1 &
    mature == 1, .N, by = rep]$N,
    save_repro = save_repro)]

if (save_gators == TRUE & t >= (tH0 - 1)) {

```

```

    save_i_data(data = gators, year = t)
  }

  ## [RECRUITMENT & GROWTH] ----
  # Update pop records for t+1 and integrate records for new recruits w/
  # existing population members
  if (t < n_years) {
    gators <- year_end(gators_t = gators)
  }

} # close t loop

saveRDS(gators, file = paste0("data/raw_data/gators_", thedate, ".RDS"))
saveRDS(pop, file = paste0("data/raw_data/pop_", thedate, ".RDS"))
}

sim_pop_before_tH0(
  n_reps = 10,
  n_years = 101,
  tH0 = 51,
  save_gators = FALSE,
  save_repro = FALSE
)

#[FUNCTION: Simulate alligator timeseries beginning first year of harvest]-----

lamda_ts <-
  sim_pop_from_tH0(
    lamda = 0.13,
    fileID = paste0("_lamda_", thedate),
    return_pop = TRUE,
    save_pop = TRUE,
    saveRDS_gators = TRUE,
    saveRDS_repro = TRUE,
    successRate = 0.875,
    n_reps = 10,
    tH0 = 51,
    n_years = 62,
    start_t = 1,
    end_t = 62
  )

```

## Appendix D

### R Code for Generating IPM Data Sets from Simulated Population Time Series

```
## Appendix D. R code for generating IPM data sets from simulated population
timeseries

rm(list = ls())
library(tibble)
library(tidyr)
library(purrr) # for map_invoke and other map fxns
library(reshape)
library(data.table) # *** ?getDTthreads #setDTthreads(4)
library(driver) # for gather_array; devtools::install_github("jsilve24/driver")
library(zoo) # for na.locf()
library(readr)
library(msm) # for truncated normal distribution (msm::rtnorm)
library(dplyr, warn.conflicts = FALSE) # for mutate
set.seed(2022)

## Set working directory when working on personal HP laptop
setwd("C:/Users/tbeja/OneDrive - University of Georgia/Dissertation/OrangeLakeIPM")

## Specify date for file names of objects saved
thedata <- strftime(Sys.Date(), "%y%m%d")
fileID <- paste0("_lamda_", thedate)

## Load replicate population timeseries records
# Abundance and count data; pop[z=1:9, t=1:151, c(N,H,phi,M,S), r=1:n_reps]
pop0 <-
  readRDS("data/raw_data/pop_ts_230506_lamda.RDS")# lamda_221102.RDS")
# Nesting data
repro0 <- readRDS("data/raw_data/repro_lamda_221102.RDS")
# Individual state data
gators0 <- readRDS("data/raw_data/gators_summ_lamda_221102.RDS")
# Length of original timeseries
n_years <- dim(pop0)[2]
# No. of stochastic replicates
n_reps <- dim(pop0)[4]
# Replicate (r) index
reps <- seq(n_reps)
# First year of harvest (tH0)
tH0 <- 51 #which(colSums(pop0[, , "H", 1]) != 0) %>% min()
# Index for years (t) of latent simulation with harvest records
harvYears <-
  tH0:(tH0 + 9) # corresponds to real OL harvest 1981-1990; Harvest data t=1:10
# Index for years (t) for summer records preceding each harvest in harvYears
summYears <- (tH0 - 1):(tH0 + 9) # correspond to OL summers 1981-1991

timeframes <- list(
  preH = c(1:(tH0 - 1)),
  postH = c(tH0:n_years),
```

```

    allYrs = c(1:n_years),
    studyYrs = summYears
  )

# harvYears correspond to real OL harvest 1981-1990; Harvest data years t=1:10
# summYears correspond to OL summers 1981-1991
#   Count & nesting data years (t=1:11): summYears[1:11]
#   MRR initial (t=1:10): summYears[1:10]
#   MRR recap/recoveries (t=2:11): summYears[2:11]

## Subsets of original latent records to years from which data will be generated
abundances <- pop0[1:5, summYears, "S",]
gators <- gators0[t_obs %in% summYears,]
repro <- repro0[year %in% summYears,]
harvests <- pop0[3:5, harvYears, "H",]

# _____
## Harvest data #####
# Simulate hypothetical reporting rates w/inter-annual variability by harvestable
size class
rH <- 0.9

# Make harvest data
repHdata <- map(seq(n_reps), function(r) {
  yH <- matrix(nrow = 3, ncol = length(harvYears))
  for (hc in 1:3) {
    # harvest class; hc[1]=3, hc[2]=4, hc[3]=5
    for (ht in seq(length(harvYears))) {
      # harvest years
      yH[hc, ht] <-
        rbinom(1, harvests[hc, ht, r], rH) #[hc, ht]
    }
  }
  return(yH)
})

# Save replicate harvest data sets (counts by size class (c=3:5) and year (t))
saveRDS(repHdata,
  file = paste0("data/processed_data/m_repHarvest", fileID, ".RDS")) #
***** output ****

## Count data #####
# Load real OL water level data (mean WL by month for June thru Sept. each year,
1980-1991)
OL_wl <- read_delim(
  "data/raw_data/USGS_monthlyWL_1980.1991",
  "\t",
  escape_double = FALSE,
  col_types = cols(year = col_integer(),
                    mo = col_integer()),
  trim_ws = TRUE
)
#summary(OL_wl$meanWL)

```

```

# Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
# 53.64  56.10   57.49   57.09   58.47   59.00
wlMean <- mean(OL_wl$meanWL) # 57.09402
wlSD <- sd(OL_wl$meanWL) # 1.512709

## Count survey water level data simulation
set.seed(2020)
# Generate water level observations for annual count surveys
# - 1st annual survey
WL1 <- rnorm(11, wlMean, wlSD) # mean & sd from real OL WL data
#rnorm(11, 56.763, 0.9895) # (based on daily USGS OL data) WL data generated from
random sample of normal dist
# - 2nd annual survey (replicate)
WL2 <-
  rnorm(11, WL1, 0.5) # for 2nd survey within year, generate counts with WL data that
varies in relation to WL in first survey
WL <-
  cbind(WL1, WL2) # combine water level data associated with counts into year x
survey rep matrix
#saveRDS(WL, file="data/processed_data/m_repCounts_WL.RDS")
# Center WL covariate data
cWL <- unname(apply(WL, 1:2, function(x)
  (x - mean(WL))))
#saveRDS(cWL, file="data/processed_data/m_repCounts_cWL.RDS") # *****
output ***

# Parameters for water level-detection probability function for count surveys
H <- c(-0.75, -0.8, 0.00091)
J <- c(-0.8,-0.8, 0.0009)
SA <- c(-1.7, -0.6, 0.0005)
AB <- c(-1.9,-0.5, 0.0001)
betas <- list(H, J, SA, AB)
pBetas <- do.call(rbind, betas)
# Compute size-specific annual detection probabilities based on WL0
# x^2 smaller means more open; - opens down/+ opens up; large makes more narrow
b.det <-
  rbind(pBetas, pBetas[4, ]) # WL-detection prob function parameters on logit scale

# Compute detection probability for each size class and survey replicate given WL
logitp <- array(dim = c(5, nrow(WL), 2))
pC <- logitp

for (c in 1:5) {
  # sizes: H, J, SA, A, B
  for (t in 1:nrow(WL)) {
    # year loop
    for (j in 1:2) {
      # w/in year survey rep loop
      logitp[c, t, j] <- b.det[c, 1] +
        b.det[c, 2] * cWL[t, j] +
        b.det[c, 3] * (cWL[t, j] ^ 2) # linear model for logit detection probability
      pC[c, t, j] <-
        1 / (1 + exp(-logitp[c, t, j])) # logit link function
    }
  }
}

```

```

    }
  }
} # close j, t, c loops
pC # detection probability by size class, year, and count survey rep

# Simulate rep count data sets
repCounts <- map(reps, function(r) {
  N <- abundances[, , r]
  C <- array(dim = c(5, ncol(N), 2))
  for (t in 1:ncol(N)) {
    # year loop
    for (c in 1:5) {
      # size class loop
      for (j in 1:2) {
        # w/in year survey rep loop
        C[c, t, j] <-
          rbinom(1, N[c, t], pC[c, t, j]) # generate count data by drawing sample
from Binom(N,p)
      }
    }
  }
  return(C)
})
save(repCounts,
      file = paste0("data/processed_data/m_repCounts", fileID, ".rdata")) # *****
output ***

#####
# Count number of mature females to lay nest annually (by rep)
nests <- repro[surviving_nests > 0,] %>%
  mutate(rep = as.factor(rep), year = as.factor(year)) %>%
  group_by(rep, year) %>%
  dplyr::summarise(N_nests = n())

# Convert to tibble of no. nests by rep(rows) and year(columns)
nestsBy_repYear <-
  pivot_wider(nests, values_from = N_nests, names_from = year)
N_nests <- nestsBy_repYear %>% ungroup() %>%
  select(!rep) %>% # remove rep col
  ungroup()
# Generate nest counts
pCL = 0.94 # probability of observing nest with clutch
# - How many nests are observed of all nests laid annually by rep
C_nests_tidy <- rbinom(length(nests$N_nests), nests$N_nests, pCL)
nesting <- bind_cols(nests, C_nests = C_nests_tidy)

clutch_tidy <- repro[surviving_eggs > 0,
                    .(year, eggs, surviving_eggs), by = rep] %>% setDF(.)

# To generate clutch data, randomly select sample of counted nests and
# sum across nests within year (by rep)
nesting$C_eggs <-
  map2_int(nesting$rep, nesting$year, function(r, t) {

```

```

    sample(x = clutch_tidy$eggs[which(clutch_tidy$rep == r &
                                     clutch_tidy$year == t)],
           size = nesting$C_nests[which(nesting$rep == r &
                                       nesting$year == t)],
           replace = FALSE) %>% sum(.)
  })

# Save tidy tibble with N_nests, C_nests, and C_eggs for each r & t
saveRDS(nesting,
        file = paste0("data/processed_data/m_repRepro", fileID, ".RDS")) #
***** output ****

## MRR data #####
# Load real OL capture records with size-specific counts by season 1975-1990
load("data/processed_data/NmarkXseason.rda") # markNxS
#markNxS[-which(markNxS$totalN == 0),] # seasons without marks removed

# Keep spring 1981-spring 1990 records
n_marksOL <- pivot_longer(
  markNxS,
  values_to = "N",
  names_to = "class",
  cols = c("totalN", "Nhatch", "Njuv", "NsubA", "Nad", "Nbull")
) %>%
  filter(year >= 1981, class != "totalN", season == "spring") %>%
  select(-S,-season) %>% # %>% pivot_wider(., values_from = N, names_from = year)
  mutate(
    class = case_when(
      class == "Nhatch" ~ 1,
      class == "Njuv" ~ 2,
      class == "NsubA" ~ 3,
      class == "Nad" ~ 4,
      TRUE ~ 5
    ),
    year = year - min(year) + 1
  )

# Total no. of marked alligators
n_marks <-
  n_marksOL %>% select(N) %>% sum(.) # 733 marks from spring 1981-1990

markYears <- summYears[1:10] # t = 50:59, OL springs 1981:1989
capYears <- markYears + 1 # t = 51:60, OL springs 1982:1990
n_years <- length(markYears) # years of initial captures
reps <- unique(gators$rep)
sizeclasses <- levels(gators$z)[1:5]
n_classes <- length(sizeclasses)

# Create vector object to record t when each i in simulated cap sample first
# "marked f(i); vector grows with addition of i's in each t/c sample
initialCap <- vector(mode = "list", length = n_reps)
set.seed(2022)
initialCap <- map(reps, function(r) {

```

```

#' Object to hold IDs for i's selected for MRR sample
marks <- vector(mode = "character", length = n_marks)

for (t in seq(n_years)) {
  # exclude t=n_years, no marking last t
  samplesN <- NULL

  # Number of gators in c, year t in real OL data
  samplesN <- n_marksOL$N[which(n_marksOL$year == t)]

  for (c in which(!is.na(samplesN))) {
    if (samplesN[c] >= 1) {
      alreadyMarked <- NULL
      whoNOTmarked <- NULL
      whoMarked <- NULL
      alreadyMarked <- marks[which(marks != "")]
      whoAlive <- gators[rep == r & t_obs == markYears[t] &
                          z == sizeclasses[c] & s == 1, ind]

      # If any i's previously marked, remove them from whoAvailable
      if (any(whoAlive %in% alreadyMarked)) {
        whoNOTmarked <- whoAlive[-which(whoAlive %in% alreadyMarked)]
      } else {
        # Otherwise, use all IDs in whoAvailable
        whoNOTmarked <- whoAlive
      }

      # If no i's available to mark
      if (length(whoNOTmarked) == 0) {
        print(paste(
          "none available for recapture",
          "t = ",
          as.numeric(t),
          "c = ",
          as.numeric(c)
        ))
        next
      } else {
        # Generate sample of latentSim pop member IDs for t/s/c initial captures
        whoMarked <- sample(
          whoNOTmarked,
          size = if_else(
            samplesN[c] <= length(whoNOTmarked),
            samplesN[c],
            as.numeric(length(whoNOTmarked))
          ),
          replace = FALSE
        )
        marks <- c(marks, whoMarked) # ind IDs

        # Make table with initial capture (f[i]) data for each i in whoMarked
        capSample <-
          bind_cols("ind" = whoMarked,

```

```

        "f_t" = markYears[t],
        "f_c" = c)
      initialCap[[r]] <- bind_rows(initialCap[[r]], capSample)
    } # close else
  } # close else
} # close c loop
} # close t loop
return(initialCap[[r]])
}) # close map() over reps
saveRDS(initialCap,
        file = paste0("data/processed_data/m_initialCap", fileID, ".RDS")) #
***** output ***

# Extract latent state records for marked ind, then because summer records
# loaded (not fall), need to account for years when i dies before summer in t
# i.e. z in 1:5 but h=0 and s=0 (i dead by summer - change z.t to 9), or
# z in 3:5 but h=1 (s=0) so that i is recovery by summer (change z.t to
6:8)
# if z in 6:8, h=0, s=0, row should be cut because individual recovered
previous summer
marked_ts <- map(reps, function(r) {
df <-
  gators[rep == r &
    ind %in% initialCap[[r]]$ind, .(t_obs, ind, z, h, s)] %>%
  filter(t_obs <= (tH0 - 1) + n_years) %>%
  mutate(., z_summ = pmap_chr(list(z, h, s), function(z, h, s) {
    case_when(
      z == "1" & h == 0 & s == 1 ~ "1",
      z == "1" & h == 0 & s == 0 ~ "9",
      z == "2" & h == 0 & s == 1 ~ "2",
      z == "2" & h == 0 & s == 0 ~ "9",
      z == "3" & h == 1 ~ "6",
      z == "3" & h == 0 & s == 1 ~ "3",
      z == "3" & h == 0 & s == 0 ~ "9",
      z == "4" & h == 1 ~ "7",
      z == "4" & h == 0 & s == 1 ~ "4",
      z == "4" & h == 0 & s == 0 ~ "9",
      z == "5" & h == 1 ~ "8",
      z == "5" & h == 0 & s == 1 ~ "5",
      z == "5" & h == 0 & s == 0 ~ "9",
      z %in% as.character(c(6:8)) ~ "9",
      z == "9" ~ "9",
      is.na(z) ~ "9"
    )
  })) %>%
  select(ind, t_obs, z_summ) %>%
  mutate(z_summ = as.factor(z_summ)) %>%
  pivot_wider(.,
    id_cols = ind,
    names_from = t_obs,
    values_from = z_summ) %>%
  as.data.frame()

```

```

    data.frame(ind = df$ind, t(na.locf(t(df[-1]))) %>% # carry last non-NA value
forward
    #mutate(pmap_dfr(., ~ na.locf(c(...)[-1]))) %>%
    inner_join(initialCap[[r]], ., by = "ind") %>%
    column_to_rownames(., "ind")
})
saveRDS(marked_ts,
        file = paste0("data/processed_data/m_marked_ts", fileID, ".RDS")) #
***** output ***

# Generate capture histories for marked individuals
# Size-specific detection probabilities
# - hatchling: based on inter-cohort mean capture. prob. estimate spring (t+1)
Woodward et al. (1987)
pH <- mean(c(0.72, 0.30, 0.85)) #for latentZ=1; 0.6233
# - juvenile recap; based on inter-cohort mean of detection prob. for
# spring (t+2) in Woodward et al. (1987)
pJ <- mean(c(0.24, 0.29, 0.16)) #for latentZ=2; 0.23
# - Pr(recap) for subadults(pSA), adults(pA), and bulls (pB); guess'timates
pSA <- 0.18 #for latentZ=3
pA <- 0.13 #for latentZ=4
pB <- 0.08 #for latentZ=5
# - Pr(recovery) of harvested i's; perfect detection assumed
ph <-
  1 # same value used for harvested subAdults, adults, bulls #for latentZ=6:8
# - Pr(recap)=0; assuming dead i's not observed
pD <- 0 #for latentZ=9
# Compile vector of stage-specific recap/recovery probabilities;
# - i.e. probability of i being observed in latent state z | being in z
p <-
  c(pH, pJ, pSA, pA, pB, rep(ph, 3), pD) %>% round(., 3) # 0.623 0.230 0.180 0.130
0.080 1.000 1.000 1.000 0.000

# Create matrix of capture histories
recap_recover <- function(z_ts) {
  y <- matrix(nrow = nrow(z_ts), ncol = capYears)
  first <- (z_ts$f_t) - min(z_ts$f_t) + 1
  for (i in 1:nrow(z_ts)) {
    y[i, first[i]] <- 1 # assign 1 at t of 1st cap occ
    if (first[i] > 1) {
      y[i, 1:(first[i] - 1)] <- NA # assign NA for each t after 1st cap
    }
  }
}
#' Populate capture history matrix (1 for live recapture, 0 if not recaptured)
for (i in 1:nrow(y)) {
  columns <-
    (first[i] + 1):length(summYears) # define y cols to populate for i
  columns0 <-
    2 + ((first[i] + 1):length(summYears)) # define marked_ts cols for z[i,t]
  # Create recap history for i
  y[i, c(columns)] <- rbinom(length(columns), 1,
                            p[as.integer(z_ts[i, (columns0)])])
}

```

```

#' No. capture years
nocc <- nrow(y) # length(studyYrs)
#' Divide capture histories into segments of a release & next recap/recovery
#' - Individual cap/release history details
chZ0 <- z_ts[, 3:max(columns0)] %>% rowwise %>%
  map_dfr(., ~ as.numeric(.x)) * y # observed states
#' Vector with no. occ each i observed (cap, recap, or recovery)
nRel <- c() # number of occasions i captured
for (i in 1:nrow(chZ0)) {
  nRel[i] <- length(which(chZ0[i,] != 0)) # no. caps/releases
}
#' List of i-specific vectors of occasions (t) i capt'd or recov'd, and released
icapTs <- list() # list of vectors (1 vector list element per i)
for (i in 1:nrow(chZ0)) {
  icapTs[[i]] <-
    which(chZ0[i,] != 0 &
          !is.na(chZ0[i,])) # vector with release occs (t)
}

#' - Decompose chZ0 into release segments, inclu release and subsequent recap
chSeg <- data.frame(matrix(nrow = sum(nRel), ncol = 7))
colnames(chSeg) <- c("ind", "capNo", "relZ", "relT",
                    "recapZ", "recapT", "last")
chSeg[, "ind"] <- c(rep(c(1:length(icapTs)), times = nRel))
for (i in 1:length(icapTs)) {
  i_rows <- which(chSeg[, "ind"] == i)

  chSeg[i_rows, "relT"] <- c(unlist(icapTs[[i]]))
  chSeg[i_rows, "relZ"] <-
    as.numeric(chZ0[i, chSeg[i_rows, "relT"]])

  chSeg[i_rows, "capNo"] <- c(1:nRel[i])
  chSeg[max(i_rows), "last"] <- 1

  if (nRel[i] >= 2) {
    chSeg[min(i_rows):(max(i_rows) - 1), "last"] <- 0
    for (j in 1:(nRel[i] - 1)) {
      chSeg[i_rows[j], c("recapT", "recapZ")] <-
        chSeg[i_rows[(j + 1)], c("relT", "relZ")]
    }
  }
  chSeg[max(i_rows), c("recapT", "recapZ")] <- c(0, 0)
} #View(chSeg)

#' Remove rows for segments(releases) with release z=6:8 (recoveries) and
#' releases in t=11 (no releases, only recap/recoveries in t=11)
relSeg <- chSeg[-which(chSeg[, "relZ"] %in% 6:8 |
                      chSeg[, "relT"] == length(capYears) + 1),]

segs <- matrix(0, nrow = nrow(relSeg), ncol = 4)
segs[, 1] <- as.numeric(unlist(relSeg["relZ"]))
segs[, 2] <- as.numeric(unlist(relSeg["relT"]))

```

```

segs[, 3] <- as.numeric(unlist(relSeg["recapZ"]))
segs[, 4] <- as.numeric(unlist(relSeg["recapT"]))
colnames(segs) <- c("r", "i", "s", "j")

# Objects for marginalized JAGS model
ch.char = apply(segs, 1, function(x)
  paste(x, collapse = ","))

ch.sum.out = t(sapply(strsplit(names(table(
  ch.char
)), split = ","), as.numeric))

fr.out = as.numeric(as.vector(table(ch.char)))

dat <-
  matrix(nrow = length(fr.out), ncol = (length(summYears) + 1))
dat[, (length(summYears) + 1)] <- fr.out

for (k in 1:nrow(dat)) {
  dat[k, ch.sum.out[k, 2]] <- ch.sum.out[k, 1]

  if (sum(ch.sum.out[k, c(3:4)]) != 0) {
    dat[k, ch.sum.out[k, 4]] <- ch.sum.out[k, 3]

    if ((ch.sum.out[k, 4] - ch.sum.out[k, 2]) >= 2) {
      dat[k, (ch.sum.out[k, 2] + 1):(ch.sum.out[k, 4] - 1)] <- 9
    }
  } else {
    dat[k, (ch.sum.out[k, 2] + 1):length(summYears)] <- 9
  }
}
return(dat)
}
## Create capture histories for marginalized MRR for rep pops
dat_rep <- map(marked_ts, ~ recap_recover(z_ts = .x))

# Get first capture occasion (t when marked) for marginalized cap history record
find.first <- function(x) {
  min(which(!is.na(x)))
}
# Get last occasion observed (as recap or recovery) of marginalized record
find.last <- function(x) {
  max(which(!is.na(x)))
}

repJM.data <- map(dat_rep, function(dat) {
  # capture-recapture data
  sumCH = dat[, seq(length(summYears))] # table of capture histories, obs by year
  sumFR = dat[, ncol(dat)] # frequency of each cap history (row)
  NsumCH = length(sumFR) # total number of capture histories
  obsCH <- sumCH
  # Get first and last capture occasion for line in summarized capture history
  fc <- apply(obsCH, 1, find.first)

```

```

lc <- apply(obsCH, 1, find.last)

repJM.data_r <- list(
  NsumCH = dim(sumCH)[1],
  obsCH = array(obsCH, dim = c(dim(sumCH)[1], dim(sumCH)[2])),
  sumf = as.vector(fc),
  sumFR = sumFR,
  one = sumFR,
  lc = as.vector(lc)
)
rm(sumCH, sumFR, NsumCH, obsCH, fc, lc)
return(repJM.data_r)
})
#names(repJM.data[[1]]) # "NsumCH" "obsCH" "sumf" "sumFR" "one" "lc"
saveRDS(repJM.data,
  file = paste0("data/processed_data/m_repJM", fileID, ".RDS")) #
***** output ****

#####

## Compile IPM datasets by population replicate #####
fileID <- "_lamda_221102" #paste0(thedate, "_lamda")

## Load data objects
# - Marginalized JAGS MRR submodel objects (repJM.data)
# -- for each [[r]], list w/ "NsumCH" "obsCH" "sumf" "sumFR" "one" "lc"
jmmrr <-
  readRDS(paste0("data/processed_data/m_repJM", fileID, ".RDS"))
jmmrr[[1]]

# - Nesting data, 2 lists: repCeggs[[r]][1:11] & repCnests[[r]][1:11]
nesting <-
  readRDS(paste0("data/processed_data/m_repRepro", fileID, ".RDS"))
repCnests <- map(unique(nesting$rep),
  function(r) {
    nesting$C_nests[which(nesting$rep == r)]
  })
repCeggs <- map(unique(nesting$rep),
  function(r) {
    nesting$C_eggs[which(nesting$rep == r)]
  })
repCnests[[1]]
repCeggs[[1]]

# - Count survey data (repCounts), with WL0[1:11,1:2] matrix and
# list count array [c=1:5, t=1:11,1:2] for each rep(r=1:n_reps)
cWL <-
  t(readRDS("data/processed_data/m_repCounts_cWL.RDS")) # centered
load(paste0("data/processed_data/m_repCounts", fileID, ".rdata"))
repCounts[[1]]

# - Harvest numbers (repHdata), list w/ [1:3,1:11] matrix for each rep (r=1:20)
repHdata <-

```

```

readRDS(paste0("data/processed_data/m_repHarvest", fileID, ".RDS"))
repHdata[[1]]

nReps <- length(unique(nesting$rep))
nYears <- 11

# Compile IPM data from all sources, by replicate
repIPMdata <-
  map(seq(nReps), function(r) {
    list(
      cWL = round(cWL, 3),
      Y = repCounts[[r]],
      R = repCnests[[r]],
      J = repCeggs[[r]],
      Y_hSA = repHdata[[r]][1, ],
      # only 10 years of data
      Y_hA = repHdata[[r]][2, ],
      # only 10 years of data
      Y_hB = repHdata[[r]][3, ],
      # only 10 years of data
      rrCH = jmmrr[[r]]$obsCH,
      NrrCH = jmmrr[[r]]$NsumCH,
      first = jmmrr[[r]]$sumf,
      last = jmmrr[[r]]$lc,
      rrFR = jmmrr[[r]]$sumFR,
      one = jmmrr[[r]]$one,
      Nyears = nYears
    )
  })
saveRDS(repIPMdata,
        file = paste0("data/processed_data/m_repIPMdata", fileID, ".RDS"))

## Create independent set of each replicate population objects
# needed for parallel runs of jags model -----
# Load list of replicate IPM data sets (n=10)
imap(readRDS("data/processed_data/m_repIPMdata_lamda_221102.RDS")[1:10],
     ~ {
       j1.unit <- list(
         file.nm = "m_IPM_jags_model_1102.jags",
         var = c(
           'mean.phi',
           'sdPhi',
           'psi',
           'lam',
           'p',
           'rH',
           'pFMN',
           'CL',
           'sdCL',
           'beta1',
           'beta2',
           'beta3'
         )
       ),

```

```

dat = list(
  "cWL" = as.matrix(.x$cWL) %>% t(),
  "Y" = structure(as.numeric(.x$Y), .Dim =
    c(5, 11, 2)),
  "R" = as.numeric(.x$R),
  "J" = as.numeric(.x$J),
  "rrCH" = as.matrix(.x$rrCH),
  "NrrCH" = as.numeric(.x$NrrCH),
  "first" = as.numeric(.x$first),
  "last" = as.numeric(.x$last),
  "rrFR" = as.numeric(.x$rrFR),
  "one" = as.numeric(.x$one),
  "Y_hSA" = as.numeric(.x$Y_hSA),
  "Y_hA" = as.numeric(.x$Y_hA),
  "Y_hB" = as.numeric(.x$Y_hB),
  "n.years" = 11L,
  "n.sizes" = 5L,
  "n.states" = 9L,
  "pN0_k" = round(c(685, 4100, 950, 1080, 720) /
    sum(c(
      685, 4100, 950, 1080, 720
    )), 3),
  "theta" = 1L
)
)
save(jl.unit, file = paste0("obelisk/rep_ipm_1102/input/rep_", .y, ".R"))
})

```

## Appendix E

### JAGS Code for Alligator IPM

```
model{
#-----
# Annual State Processes
#-----
# Initial size class abundances summer t=1

N0_k ~ dunif(2000, 30000)

for (c in 1:n.sizes) {
  X[c] ~ dgamma(pN0_k[c], theta)
  Nsumm[c,1] <- round(N0_k * p0_k[c])
}
p0_k[1:n.sizes] <- X[1:n.sizes] / (sum(X[1:n.sizes]))

for (z in 6:n.states) {
  Nsumm[z,1] <- 0
}

Ntot[1] <- sum(Nsumm[1:5, 1])

#No. nests based on proportion of ad+ pop. is mature nesting female
Nnests[1] ~ dbin(pFMN, sum(Nsumm[4,1],Nsumm[5,1]))

#Each nest produces clutch of eggs with expected clutch size=CL
Neggs[1] <- J[1] + round((Nnests[1]-R[1])*CL[1])

#Some portion of eggs successfully produces a hatchling to enter pop in t+1
Nrecruits[1] ~ dbin(phiEgg, Neggs[1])

for (y in 1:(n.years-1)) {
  Ntrans[1,y] ~ dbin(psi[1], Nsumm[1,y])
  Ntrans[2,y] ~ dbin(psi[2], Nsumm[2,y])
  Ntrans[3,y] ~ dbin(psi[3], Nsumm[3,y])
  Ntrans[4,y] ~ dbin(psi[4], Nsumm[4,y])

  Nfall[1,y] <- Nrecruits[y] + Nsumm[1,y] - Ntrans[1,y]
  Nfall[2,y] <- Nsumm[2,y] - Ntrans[2,y] + Ntrans[1,y]
  Nfall[3,y] <- Nsumm[3,y] - Ntrans[3,y] + Ntrans[2,y]
  Nfall[4,y] <- Nsumm[4,y] - Ntrans[4,y] + Ntrans[3,y]
  Nfall[5,y] <- Nsumm[5,y] + Ntrans[4,y]
  Nfall[6,y] <- 0
  Nfall[7,y] <- 0
  Nfall[8,y] <- 0
  Nfall[9,y] <- Nsumm[9,y] + Nsumm[6,y] + Nsumm[7,y] + Nsumm[8,y]

  # Hunting season
  H[1,y] ~ dbin(lam, Nfall[3,y])
  H[2,y] ~ dbin(lam, Nfall[4,y])
}
```

```

H[3,y] ~ dbin(lam, Nfall[5,y])

NpostH[1,y] <- Nfall[1,y]
NpostH[2,y] <- Nfall[2,y]
NpostH[3,y] <- Nfall[3,y] - H[1,y]
NpostH[4,y] <- Nfall[4,y] - H[2,y]
NpostH[5,y] <- Nfall[5,y] - H[3,y]
NpostH[6,y] <- H[1,y]
NpostH[7,y] <- H[2,y]
NpostH[8,y] <- H[3,y]
NpostH[9,y] <- Nfall[9,y]
}

for (t in 2:n.years){
  Nsumm[1,t] ~ dbin(phiH[(t-1)], NpostH[1,(t-1)])
  Nsumm[2,t] ~ dbin(phiJ[(t-1)], NpostH[2,(t-1)])
  Nsumm[3,t] ~ dbin(phiSA[(t-1)], NpostH[3,(t-1)])
  Nsumm[4,t] ~ dbin(phiA[(t-1)], NpostH[4,(t-1)])
  Nsumm[5,t] ~ dbin(phiB[(t-1)], NpostH[5,(t-1)])
  Nsumm[6,t] <- NpostH[6,(t-1)]
  Nsumm[7,t] <- NpostH[7,(t-1)]
  Nsumm[8,t] <- NpostH[8,(t-1)]
  Nsumm[9,t] <- NpostH[9,(t-1)] + (NpostH[1,(t-1)] - Nsumm[1,t]) +
                                     (NpostH[2,(t-1)] - Nsumm[2,t]) +
                                     (NpostH[3,(t-1)] - Nsumm[3,t]) +
                                     (NpostH[4,(t-1)] - Nsumm[4,t]) +
                                     (NpostH[5,(t-1)] - Nsumm[5,t])

  Ntot[t] <- sum(Nsumm[1:5, t])
}

for (t in 2:n.years){
  # Summer reproduction
  # No. nests based on proportion of ad+ pop. is mature nesting female
  Nnests[t] ~ dbin(pFMN, sum(Nsumm[4,t],Nsumm[5,t]))

  # Each nest produces clutch of eggs with expected clutch size=CL
  Neggs[t] <- trunc(sum(J[t], (Nnests[t]-R[t])*CL[t]))

  # Some portion of eggs successfully produces a hatchling to enter pop in t+1
  Nrecruits[t] ~ dbin(phiEgg, Neggs[t])
}
#-----
# Observation Processes
#-----
## Likelihood for COUNT SURVEY DATA -----
for (c in 1:n.sizes) { # loop through size classes
  for (t in 1:n.years) { # loop through years
    for (j in 1:2) { # loop through replicate surveys within year

      # Count survey detection prob on the logit scale is a linear fxn of
      # centered WL and size-spec. regression params (betas)
      logit(pC[c,t,j]) <- beta1[c] + beta2[c]*cWL[t,j] + beta3[c]*pow(cWL[t,j],2)
    }
  }
}

```

```

# Survey counts based on true summer abundance and survey covariate data
Y[c,t,j] ~ dbin(pC[c,t,j], Nsumm[c,t])

# Calculate deviance for observed and replicate data
# Replicate data generated from likelihood for deviance test
Y.new[c,t,j]~ dbin(pC[c,t,j], Nsumm[c,t])
# Pearson's residuals for observed data
resid[c,t,j] <- (Y[c,t,j] - Nsumm[c,t]*pC[c,t,j]) /
                sqrt(Nsumm[c,t]*pC[c,t,j]*(1-pC[c,t,j]))
# Pearson's residual for replicate data
resid.new[c,t,j] <- (Y.new[c,t,j] - Nsumm[c,t]*pC[c,t,j]) /
                  sqrt(Nsumm[c,t]*pC[c,t,j]*(1-pC[c,t,j]))
# Calc Pearson's sq'd residual w/ 0.1 added to denominator to avoid
dividing by 0
residSq[c,t,j] <- pow((Y[c,t,j] - Nsumm[c,t]*pC[c,t,j]), 2) /
                 (Nsumm[c,t]*pC[c,t,j]*(1-pC[c,t,j]) + 0.1) # for
observed data
residSq.new[c,t,j] <- pow((Y.new[c,t,j] - Nsumm[c,t]*pC[c,t,j]), 2) /
                    (Nsumm[c,t]*pC[c,t,j]*(1-pC[c,t,j]) + 0.1) # for
rep data

    } # close j
  } # close t
} # close c

## Likelihood for NEST SURVEY DATA -----
for (t in 1:n.years) {
  R[t] ~ dbin(pCL, Nnests[t])
  J[t] ~ dpois(R[t] * CL[t])
}
## Likelihood for RECAPTURE-RECOVERY DATA -----
for (y in 1:(n.years - 1)) {
  # Define transition matrix for each NsumCH, compiled into array
  tr[1,y,1] = (1 - psi[1]) * phiH[y]
  tr[1,y,2] = psi[1] * phiJ[y]
  tr[1,y,3] = 0
  tr[1,y,4] = 0
  tr[1,y,5] = 0
  tr[1,y,6] = 0
  tr[1,y,7] = 0
  tr[1,y,8] = 0
  tr[1,y,9] = (1 - psi[1]) * (1 - phiH[y]) + psi[1] * (1 - phiJ[y])
  tr[2,y,1] = 0
  tr[2,y,2] = (1 - psi[2]) * phiJ[y]
  tr[2,y,3] = psi[2] * (1 - lam) * phiSA[y]
  tr[2,y,4] = 0
  tr[2,y,5] = 0
  tr[2,y,6] = psi[2] * lam
  tr[2,y,7] = 0
  tr[2,y,8] = 0
  tr[2,y,9] = (1 - psi[2]) * (1 - phiJ[y]) + psi[2] * (1 - lam)*(1 - phiSA[y])
  tr[3,y,1] = 0
  tr[3,y,2] = 0

```

```

tr[3,y,3] = (1 - psi[3]) * (1 - lam) * phiSA[y]
tr[3,y,4] = psi[3] * (1 - lam) * phiA[y]
tr[3,y,5] = 0
tr[3,y,6] = (1 - psi[3]) * lam
tr[3,y,7] = psi[3] * lam
tr[3,y,8] = 0
tr[3,y,9] = (1-psi[3]) * (1-lam) * (1-phiSA[y]) + psi[3]*(1-lam)*(1-phiA[y])
tr[4,y,1] = 0
tr[4,y,2] = 0
tr[4,y,3] = 0
tr[4,y,4] = (1 - psi[4]) * (1 - lam) * phiA[y]
tr[4,y,5] = psi[4] * (1 - lam) * phiB[y]
tr[4,y,6] = 0
tr[4,y,7] = (1 - psi[4]) * lam
tr[4,y,8] = psi[4] * lam
tr[4,y,9] = (1-psi[4]) * (1-lam) * (1-phiA[y]) + psi[4]*(1-lam)*(1-phiB[y])
tr[5,y,1] = 0
tr[5,y,2] = 0
tr[5,y,3] = 0
tr[5,y,4] = 0
tr[5,y,5] = (1 - lam) * phiB[y]
tr[5,y,6] = 0
tr[5,y,7] = 0
tr[5,y,8] = lam
tr[5,y,9] = (1 - lam) * (1 - phiB[y])
tr[6,y,1] = 0
tr[6,y,2] = 0
tr[6,y,3] = 0
tr[6,y,4] = 0
tr[6,y,5] = 0
tr[6,y,6] = 0
tr[6,y,7] = 0
tr[6,y,8] = 0
tr[6,y,9] = 1
tr[7,y,1] = 0
tr[7,y,2] = 0
tr[7,y,3] = 0
tr[7,y,4] = 0
tr[7,y,5] = 0
tr[7,y,6] = 0
tr[7,y,7] = 0
tr[7,y,8] = 0
tr[7,y,9] = 1
tr[8,y,1] = 0
tr[8,y,2] = 0
tr[8,y,3] = 0
tr[8,y,4] = 0
tr[8,y,5] = 0
tr[8,y,6] = 0
tr[8,y,7] = 0
tr[8,y,8] = 0
tr[8,y,9] = 1
tr[9,y,1] = 0

```

```

tr[9,y,2] = 0
tr[9,y,3] = 0
tr[9,y,4] = 0
tr[9,y,5] = 0
tr[9,y,6] = 0
tr[9,y,7] = 0
tr[9,y,8] = 0
tr[9,y,9] = 1
# Define observation process array, observation matrix assigned to each Nint
rho[1,y,1] = p[1]
rho[1,y,2] = 0
rho[1,y,3] = 0
rho[1,y,4] = 0
rho[1,y,5] = 0
rho[1,y,6] = 0
rho[1,y,7] = 0
rho[1,y,8] = 0
rho[1,y,9] = 1 - p[1]
rho[2,y,1] = 0
rho[2,y,2] = p[2]
rho[2,y,3] = 0
rho[2,y,4] = 0
rho[2,y,5] = 0
rho[2,y,6] = 0
rho[2,y,7] = 0
rho[2,y,8] = 0
rho[2,y,9] = 1 - p[2]
rho[3,y,1] = 0
rho[3,y,2] = 0
rho[3,y,3] = p[3]
rho[3,y,4] = 0
rho[3,y,5] = 0
rho[3,y,6] = 0
rho[3,y,7] = 0
rho[3,y,8] = 0
rho[3,y,9] = 1 - p[3]
rho[4,y,1] = 0
rho[4,y,2] = 0
rho[4,y,3] = 0
rho[4,y,4] = p[4]
rho[4,y,5] = 0
rho[4,y,6] = 0
rho[4,y,7] = 0
rho[4,y,8] = 0
rho[4,y,9] = 1 - p[4]
rho[5,y,1] = 0
rho[5,y,2] = 0
rho[5,y,3] = 0
rho[5,y,4] = 0
rho[5,y,5] = p[5]
rho[5,y,6] = 0
rho[5,y,7] = 0
rho[5,y,8] = 0

```

```

rho[5,y,9] = 1-p[5]
rho[6,y,1] = 0
rho[6,y,2] = 0
rho[6,y,3] = 0
rho[6,y,4] = 0
rho[6,y,5] = 0
rho[6,y,6] = 1
rho[6,y,7] = 0
rho[6,y,8] = 0
rho[6,y,9] = 0
rho[7,y,1] = 0
rho[7,y,2] = 0
rho[7,y,3] = 0
rho[7,y,4] = 0
rho[7,y,5] = 0
rho[7,y,6] = 0
rho[7,y,7] = 1
rho[7,y,8] = 0
rho[7,y,9] = 0
rho[8,y,1] = 0
rho[8,y,2] = 0
rho[8,y,3] = 0
rho[8,y,4] = 0
rho[8,y,5] = 0
rho[8,y,6] = 0
rho[8,y,7] = 0
rho[8,y,8] = 1
rho[8,y,9] = 0
rho[9,y,1] = 0
rho[9,y,2] = 0
rho[9,y,3] = 0
rho[9,y,4] = 0
rho[9,y,5] = 0
rho[9,y,6] = 0
rho[9,y,7] = 0
rho[9,y,8] = 0
rho[9,y,9] = 1
} # close y

# Loop through capture segments
for (k in 1:NrrCH) {
  pz[k, first[k], 1] <- equals(rrCH[k, first[k]], 1)
  pz[k, first[k], 2] <- equals(rrCH[k, first[k]], 2)
  pz[k, first[k], 3] <- equals(rrCH[k, first[k]], 3)
  pz[k, first[k], 4] <- equals(rrCH[k, first[k]], 4)
  pz[k, first[k], 5] <- equals(rrCH[k, first[k]], 5)
  pz[k, first[k], 6] <- 0
  pz[k, first[k], 7] <- 0
  pz[k, first[k], 8] <- 0
  pz[k, first[k], 9] <- 0

  for (m in first[k]:(last[k]-1)) {
    for (z in 1:n.states) {

```

```

        pz[k,(m+1),z] <- inprod(pz[k,m, ], tr[ ,m,z]) * rho[z,m,rrCH[k,(m+1)]]
    }
}
lik[k] <- sum(pz[k, last[k], ])
one[k] ~ dbin(lik[k], rrFR[k])
}
## Likelihood for HARVEST DATA -----
for (y in 1:(n.years-1)) {
  Y_hSA[y] ~ dbin(rH, H[1,y])
  Y_hA[y] ~ dbin(rH, H[2,y])
  Y_hB[y] ~ dbin(rH, H[3,y])
}

## Priors -----
rH ~ dunif(0.5, 1) # hunter harvest reporting rate

lam ~ dunif(0, 0.5) # harvest probability

for (v in 1:(n.sizes-1)){
  psi[v] ~ dunif(0, 1) # transition probabilities
}

for (l in 1:10) { # survival probabilities
  phiH[l] ~ dnorm(mean.phi[1], tauPhi[1]) T(0,1)
  phiJ[l] ~ dnorm(mean.phi[2], tauPhi[2]) T(0,1)
  phiSA[l] ~ dnorm(mean.phi[3], tauPhi[3]) T(0,1)
  phiA[l] ~ dnorm(mean.phi[4], tauPhi[4]) T(0,1)
  phiB[l] ~ dnorm(mean.phi[5], tauPhi[5]) T(0,1)
}

for (c in 1:n.sizes){
  mean.phi[c] ~ dunif(0, 1) # for mean state-spec. survival
  sdPhi[c] ~ dunif(0, 1)
  tauPhi[c] <- pow(sdPhi[c], -2)

  p[c] ~ dunif(0, 1) # for mean state-spec. recapture
}

# Linear model params for count survey detection probability
for (v in 1:(n.sizes-1)){
  beta1[v] ~ dnorm(0, 0.37)
  beta2[v] ~ dnorm(0, 0.37)
  beta3[v] ~ dnorm(0, 0.37)
}
beta1[5] <- beta1[4]
beta2[5] <- beta2[4]
beta3[5] <- beta3[4]

for (t in 1:n.years){
  CL[t] ~ dnorm(muCL, tauCL) T(0,)
  disc_N[t] <- abs(Ntot[t] - trueNtot[t]) # annual total population size

  for (z in 1:9){

```

```

    disc_Nz[z,t] <- abs(Nsumm[z,t] - trueNsumm[z,t])
  }
}

pFMN ~ dunif(0, 1) # prior for proportion of adult+ pop that is nesting female
pCL ~ dunif(0, 1) # prior for nest detection prob
muCL ~ dunif(30, 40) # prior for expected clutch size
tauCL <- pow(sdCL,-2) # precision for clutch size
sdCL ~ dunif(0, 10) # prior for SD of clutch size
phiEgg ~ dunif(0, 1) # prior for egg survival rate

for (v in 1:4){
  disc_p[v] <- abs(p[v] - true_p[v])
  disc_psi[v] <- abs(psi[v] - true_psi[v])
  disc_mean.phi[v] <- abs(mean.phi[v] - true_mean.phi[v])
}
disc_p[5] <- abs(p[5] - true_p[5])
disc_mean.phi[5] <- abs(mean.phi[5] - true_mean.phi[5])
disc_pFMN <- abs(pFMN - true_pFMN)
disc_phiEgg <- abs(phiEgg - truePhiEgg)
disc_rH <- abs(rH - true_rH)
disc_lam1 <- abs(lam - true_lam1)
disc_lam2 <- abs(lam - true_lam2)
disc_pCL <- abs(pCL - true_pCL)

# Fit of observed and replicate data (MAYBE SUMMARIZE BY c in future...)
fit <- sum(resid[,,]) # sum of Pearson's residuals for observed data
fit.new <- sum(resid.new[,,]) # sum of Pearson's residuals for replicate data
fitSq <- sum(residSq[,,]) # sum of squared Pearson's residual for observed
data
fitSq.new <- sum(residSq.new[,,]) # sum of sq'd Pearson's residual for rep data

# Bayesian p-value (deviance measure)
B_pval <- step(fit.new - fit) # based on Pearson's residuals
B_pvalSq <- step(fitSq.new - fitSq) # based on squared Pearson's residual

} # end jags model

# Function to generate initial values -----
init.fun <- function(n){
  set.seed(2023)
  map(1:n, function(n) {
    beta1 = c(runif(2, -1, -0.5), runif(2, -2, -1)) %>% sort(., decreasing = TRUE)
    beta2 = runif(4, -0.9, 0) %>% sort(., decreasing = FALSE)
    beta3 = runif(4, 0.00009, 0.001) %>% sort(., decreasing = TRUE)
    beta1[5] <- beta1[4]
    beta2[5] <- beta2[4]
    beta3[5] <- beta3[4]

  })

  list(
    N0_k = runif(1, 19000, 30000),
    muCL = runif(1, 30, 40),
    pCL = runif(1, 0.7, 1), # latent value = 0.94

```

```
pFMN = runif(1, 0.07, 0.2), # latent value ~ 0.15
phiEgg = runif(1, 0.1, 0.6), # latent value = 0.452*0.875
lam = runif(1, 0.1, 0.2),
mean.phi = c(runif(1, 0.3, 0.6), runif(4, 0.8, 0.99)),
psi = c(runif(1, 0.8, 0.99), runif(2, 0.1, 0.3), runif(1, 0.01, 0.1)),
rH = runif(1, 0.8, 1),
beta1 = beta1, beta2 = beta2, beta3 = beta3)
})
}
```

Initial values generated for three MCMC chains

JAGS Label	Parameter	Chain 1	Chain 2	Chain 3
N0_k	$N_{0c}$	20984.73	22743.27	21874.05
lam	$\lambda$	0.1889625	0.1801452	0.1116490
psi[1]	$\Psi_H$	0.97728759	0.88517508	0.95851674
psi[2]	$\Psi_J$	0.24259088	0.15294634	0.23315939
psi[3]	$\Psi_{SA}$	0.22617037	0.18185350	0.20882384
psi[4]	$\Psi_A$	0.07718045	0.02751371	0.06960627
mean.phi[1]	$\bar{\phi}_H$	0.3959545	0.4789283	0.5611792
mean.phi[2]	$\bar{\phi}_J$	0.9347130	0.9856334	0.8244474
mean.phi[3]	$\bar{\phi}_{SA}$	0.9193488	0.8623399	0.9587218
mean.phi[4]	$\bar{\phi}_A$	0.8832528	0.9529842	0.8451615
mean.phi[5]	$\bar{\phi}_B$	0.8645802	0.8061399	0.8855795
phiEgg	$\phi_{egg}$	0.2724242	0.5442485	0.4469968
rH	$r_H$	0.8222901	0.9086975	0.9747025
muCL	$\mu_{CL}$	39.9927300	36.6856300	33.3033600
pCL	$p_{CL}$	0.9525224	0.8152762	0.7991692
pFMN	$p_{FMN}$	0.08854438	0.10056470	0.08200593
beta1[1]	$\beta_{1,H}$	-0.7666930	-0.8633557	-0.5324481
beta1[2]	$\beta_{1,J}$	-0.8324045	-0.9507410	-0.6129812
beta1[3]	$\beta_{1,SA}$	-1.6038800	-1.2424705	-1.0031167
beta1[4]	$\beta_{1,A}$	-1.8371824	-1.3364079	-1.1773742
beta1[5]	$\beta_{1,B}$	-1.8371824	-1.3364079	-1.1773742
beta2[1]	$\beta_{2,H}$	-0.87264740	-0.48694810	-0.61303228
beta2[2]	$\beta_{2,J}$	-0.79120360	-0.29304130	-0.55327547
beta2[3]	$\beta_{2,SA}$	-0.51645090	-0.26953770	-0.54746519
beta2[4]	$\beta_{2,A}$	-0.34392790	-0.24807500	-0.09077598
beta2[5]	$\beta_{2,B}$	-0.34392790	-0.24807500	-0.09077598
beta3[1]	$\beta_{3,H}$	0.00087471	0.00090043	0.00060340
beta3[2]	$\beta_{3,J}$	0.00052345	0.00083172	0.00052870
beta3[3]	$\beta_{3,SA}$	0.00032952	0.00074194	0.00027991
beta3[4]	$\beta_{3,A}$	0.00022548	0.00071898	0.00014925
beta3[5]	$\beta_{3,B}$	0.00022548	0.00071898	0.00014925

## Appendix F

### R Code for Alligator Harvest Policy Function Optimization

```
## Appendix F. R Code for Alligator Harvest Policy Function Optimization

# The following code:
# 1. Specifies a function to simulate the population through the year preceding
#    initiation of annual harvest (t = 1:(tH0-1)), then saves the pop and gators
#    objects
# 2. Specifies function to take pop and gators objects and simulate population
#    over 50 years with harvest (t = tH0:101), then computes and returns a fitness
#    score
# 3. Sets-up, then runs ga() and prints a summary of the results

# [FUNCTION: Simulate time series for years before harvest (1:(tH0-1))-----
# and save gators and pop objects; then, run sim_pop_from_tH0]
sim_pop_before_tH0 <- function(n_reps = 50, n_years = 101, tH0 = 51,
                              save_gators = FALSE, save_repro = FALSE,
                              phi0 = c(0.41, 0.843, 0.8552, 0.9057, 0.823), #
baseline annual survival probs
                              b_k = c(-1.4272, -2.0244, -4.129, -11.715, -3.264), #
slopes for DD survival
                              b_D = 39.622, # slope for DD puberty
                              adD_0 = 0.193) # baseline adult density for DD
survival and puberty
{
  # Define size classes based on total length (TL cm)
  size_class <- cut(c(1:500), breaks = c(-Inf, 30, 122, 183, 274, Inf),
                   right = FALSE, include.lowest = FALSE, labels = c(1:5))

  # Latent states; 5 size classes(1:5) + three harvest classes(6:8) + dead(9)
  state <- factor(1:9, labels = c(levels(size_class), c(6:9)))

  #' Area of Orange Lake
  OL.ha <- 5251.5 # hectares

  #'[FUNCTION: Size-specific sex assignment]
  assign_sex <- function(n, sex_ratio) {
    sex <- rbinom(as.numeric(n), 1, sex_ratio) + 1 # 1=female, 2=male
    return(sex)
  }

  #'[FUNCTIONS: Convert SVL to TL or vice versa based on sex-specific conversion]
  make_TL <- function(size, sex) {
    a_sv1TL <- c(2.2390, 2.3121)
    b_sv1TL <- c(0.9707, 0.9622)
    TL <- a_sv1TL[sex] * (size^b_sv1TL[sex])
    return(TL)
  }
  make_SVL <- function(size, sex) {
```

```

# a & b parameter values from Table 7 Woodward et al. 1992; c(F,M)
a_svlTL <- c(2.2390, 2.3121)
b_svlTL <- c(0.9707, 0.9622)
SVL <- (size/a_svlTL[sex])^(1/b_svlTL[sex])
return(SVL)
}

#[FUNCTION: Alligator growth model, Baker-form of Schnute model]
grow <- function(sex, Ym) {
  tau = c(0, 45) # age (yrs) at hatchling and max life expectancy
  deltaT = 1 # duration of growth period
  y1 = 12.5 # SVL at hatching (cm)
  y2 = c(135.9, 186.9) # terminal SVL c(F,M)
  a = c(0.11, 0.09); b = c(0.72, 0.69) # growth rate(a) and shape(b) c(F,M)
  modelErr = c(5.9, 7.42) # model error c(F,M)

  # Compute expected SVL after annual growth, use to draw realized value from
  # normal distribution, then convert to TL if below terminal size for sex;
  # otherwise, keep last TL
  iYr <- (((Ym^b[sex]) * exp(-a[sex]*deltaT)) +
    ((y2[sex]^b[sex]) - (y1^b[sex])*exp(-a[sex]*(tau[2] - tau[1])))) *
    ((1 - exp(-a[sex]*deltaT)) /
    (1 - exp(-a[sex]*(tau[2] - tau[1])))))^(1/b[sex]) %>%
    rtnorm(n = length(.), mean = ., sd = sqrt(modelErr[sex]), lower = Ym)
  newTL <- ifelse(Ym <= y2[sex],
    make_TL(size = iYr, sex = sex),
    make_TL(size = Ym, sex = sex))

  return(round(as.numeric(newTL), 1)) # TL(cm) for t+1
}

#[FUNCTION: Create initial population, no replicates]
make_founders <- function(N0_k) {
  set.seed(2021)

  # Draw sex variable for each founding population member
  p_male <- c(0.5, 0.63, 0.53, 0.53, 0.90) # size class-specific ratio M to F

  pop <- map(as.integer(unique(size_class)),
    function(c) tibble(size_class = rep(c, N0_k[c]),
      sex = assign_sex(n = N0_k[c],
        sex_ratio = p_male[c]) %>%
        as.integer) %>%
    arrange(., sex) %>% mutate(TL = 0))

  size_lims <- c(18, 30, 122, 183, 274, 300)

  svl_lims <- array(c(size_lims[1:5] %>% make_SVL(size = ., sex = 1),
    size_lims[2:6] %>% make_SVL(size = ., sex = 1),
    size_lims[1:5] %>% make_SVL(size = ., sex = 2),
    size_lims[2:6] %>% make_SVL(size = ., sex = 2)),
    dim = c(5,2,2),
    dimnames = list(c(), c("min", "max"), c("F", "M")))

```

```

pop <- map_dfr(seq(pop), function(c) pop[[c]] %>% setDT(.))

pop[ , TL:= map2_dbl(pop$sex, pop$size_class,
  ~ runif(1, min = svl_lims[.y, "min", .x],
    max = svl_lims[.y, "max", .x]) %>%
  make_TL(size = ., sex = .x))]

founders <- tibble(sex = pop$sex, TL = pop$TL) %>%
  mutate(z = size_class[TL] %>% factor(., levels = state)) %>%
#size_class[TL]) %>%
  arrange(., desc(z), sex, desc(TL)) %>%
  mutate(t_recruit = as.integer(1), .before = 4) %>%
  mutate(mature = if_else(sex == as.integer(1),
    as.integer(0),
    as.integer(NA))) %>%
  mutate(f = as.integer(NA)) %>%
  mutate(ind = as.character(1:sum(N0_k)), .before = 1) %>% setDT
return(founders)
}

#[FUNCTION: ...]
list2cols <- function(x) { x %>% unlist %>%
  matrix(., nrow = n_reps, byrow = TRUE) %>% t() }

#[FUNCTION: compute density-dependent size-specific annual survival]
dd_phi <- function(adD_0, b_c, phi0, D_t) {
  suppressMessages(map_dfc(D_t, ~
    plogis(q = qlogis(phi0) + (b_c * (log10(.x) -
log10(adD_0)))) %>%
    round(digits = 4) %>% c(., rep(0,4))) %>%
as.matrix() %>% unname)
}

###[FUNCTION:nual survival outside harvest for each i based on z and t(due to dd)
get_phi_it <- function(phi_ct, z_it) {
  phi_it <- phi_ct[as.integer(z_it)]
  return(phi_it)
}

#[FUNCTION: Probability that adult female reaches sexual maturity given TL]
# her_TL=180.5; adult_density=0.193
puberty <- function(her_TL, adD_t = NULL) {
  base_offset <- -(-17.46644/0.087134877) # baseline TL offset for OL (200.4529)
  OL_slope <- 0.087134877 # slope logit(pM) by female TL

  if (is.null(adD_t)) {
    logit_pM <- OL_slope * (her_TL - base_offset)
  } else {
    DD_offset <- base_offset + (b_D * (log10(adD_t) - log10(adD_0)))
    logit_pM <- OL_slope * (her_TL - DD_offset)
  }
}

```

```

pM <- 1 / (1 + exp(-(logit_pM))) # convert to probability scale
sexually_mature <- rbinom(length(pM), 1, prob = pM)
return(sexually_mature)
}

#[FUNCTION: ...]
nesting <- function(N_adFM, save_repro) {
  mean_clutch = 33
  repro <- imap_dfr(N_adFM, ~ {
    nests <- rbinom(.x, 1, prob = 0.398)
    surviving_nests <- rbinom(nests, 1, prob = 0.452) * nests
    eggs <- rpois(.x, mean_clutch) * surviving_nests
    surviving_eggs <- rbinom(length(eggs), eggs, prob = 0.875)
    repro <- data.table(nests, surviving_nests, eggs,
                       surviving_eggs, rep = .y, year = t))
  if (save_repro == TRUE & t >= (tH0 - 1)){
    if (t == (tH0-1)) {saveRDS(repro, file = "repro_040422.RDS")}
    } else {
    old <- readRDS(file = "repro_040422.RDS")
    data <- repro
    updated <- bind_rows(old, data)
    saveRDS(updated, file = "repro_040422.RDS")
    }
  }
}
return(repro$surviving_eggs)
}

#[FUNCTION: make pop_members-like table for new hatchlings to add to survivors of
t, in t+1]
recruitment <- function(n_recruits, last_id, year_hatched, pop_rep) {
  #[FUNCTION: for ...]
  f_hatch_TL <- function(n_hatched, sex) {
    svl <- runif(n_hatched,
                min = make_SVL(18,sex),
                max = make_SVL(30,sex))
    hatchling_TLs <- make_TL(size = svl,
                             sex = sex)
    return(hatchling_TLs)
  }
  recruits <- tibble(sex = as.integer(assign_sex(n = n_recruits,
                                                sex_ratio = 0.5)),
                    TL = as.double(f_hatch_TL(n_hatched = n_recruits,
                                              sex = sex)) ,
                    z = factor(as.integer(size_class[TL]), levels = 1:9),
                    t_recruit = rep(as.integer(year_hatched+1),
                                    length = n_recruits),
                    mature = if_else(sex == as.integer(1), as.integer(0),
                                     as.integer(NA)),
                    f = as.integer(NA),
                    rep = pop_rep) %>% #factor(pop_rep, levels = seq(n_reps))
  arrange(., desc(z), sex, desc(TL)) %>%
  add_column(.,
             ind = as.character((last_id+1):(last_id+n_recruits)),

```

```

        .before = 1) %>%
      setDT(.)
      return(recruits)
    }

#' [FUNCTION: Based on i records for year t, generate i records object for t+1]
year_end <- function(gators_t) {
  # Remove gators that were dead at the beginning of t
  gators_t1 <- gators_t[z != "9", ]

  # Convert state z from factor to integer for ease in next steps
  gators_t1[, z := as.integer(z)]

  # Harvest recoveries at the beginning of t now dead (for t+1)
  gators_t1[z %in% 6:8, z := 9]

  # Update records for harvested gators
  gators_t1[h == 1, ':=' (z = z + 3, TL = 0, f = 0)]

  # Update state for gators that died of non-harvest mortality in t
  gators_t1[which(z <= 5 & h == 0 & s == 0), ':=' (z = 9, TL = 0, f = 0)]

  # Grow surviving individuals
  gators_t1[s == 1, TL := grow(sex = gators_t1[s==1, sex],
                              Ym = make_SVL(size = gators_t1[s==1, TL],
                                             sex = gators_t1[s==1, sex]))]

  # Update state for survivors
  gators_t1[s == 1, z := as.integer(size_class[gators_t1[s == 1, TL]])]
  gators_t1[, z := factor(z, levels = state)]

  # Reset fecundity
  gators_t1$f <- as.integer(NA)

  # Updated records for t+1
  updated_gators <- gators_t1[,c("ind", "sex", "TL", "z", "t_recruit",
                                "mature", "f", "rep")]

  pop_t1 <- gators_t[, sum(f, na.rm = TRUE), by = rep] %>% pull(V1) %>%
  imap(., function(n, r) {
    if (n == 0) { updated_gators[rep == r, ]
    } else {
      recruitment(n_recruits = n,
                  last_id = max(as.integer(gators_t[rep == r, ind])),
                  year_hatched = t,
                  pop_rep = r) %>%
      bind_rows(updated_gators[rep == r, ], .)
    }
  }) %>% rbindlist()
  return(pop_t1)
}

#' Create array for annual state-specific records

```



```

## [NESTING] ----
gators[s == 1 & mature == 1,
      f := nesting(N_adFM = gators[s==1 & mature==1, .N, by=rep]$N,
                  save_repro = save_repro)]

if (save_gators == TRUE & t >= (tH0 - 1)) {
  save_i_data(data = gators, year = t)
}

## [RECRUITMENT & GROWTH] ----
# Update pop records for t+1 and integrate records for new recruits w/
# existing population members
if (t < n_years) {
  gators <- year_end(gators_t = gators)
}

} # close t loop

saveRDS(gators, file = paste0("gators_", thedate, ".RDS"))
saveRDS(pop, file = paste0("pop_", thedate, ".RDS"))
}

#[FUNCTION: Simulate alligator timeseries beginning first year of harvest]-----
sim_pop_from_tH0 <- function(x = NULL, lamda = NULL, return_pop = NULL,
                             save_pop = NULL, fileID = NULL,
                             n_reps = 50, tH0 = 51, n_years = 101) {

  gators <- readRDS(paste0("gators_", thedate, ".RDS"))
  pop <- readRDS(paste0("pop_", thedate, ".RDS"))

  phi0 = c(0.41, 0.843, 0.8552, 0.9057, 0.823) # baseline annual survival probs
  b_k = c(-1.4272, -2.0244, -4.129, -11.715, -3.264) # slopes for DD survival
  b_D = 39.622 # slope for DD puberty
  adD_0 = 0.193 # baseline adult density for DD survival and puberty

  if (!missing(x)) {
    harvest_policy <- x[1:2]
    Qmax <- x[3]
  } else {
    if (!missing(lamda)) {
      harvest_policy <- lamda
    } else {
      harvest_policy <- 0.13
    }
  }

  mean_clutch = 33 # average clutch size

  # Define size classes based on total length (TL cm)
  size_class <- cut(c(1:500), breaks = c(-Inf, 30, 122, 183, 274, Inf),
                   right = FALSE, include.lowest = FALSE, labels = c(1:5))

  # Latent states; 5 size classes(1:5) + three harvest classes(6:8) + dead(9)

```

```

state <- factor(1:9, labels = c(levels(size_class), c(6:9)))

#' Area of Orange Lake
OL.ha <- 5251.5 # hectares

#'[FUNCTION: Size-specific sex assignment]
assign_sex <- function(n, sex_ratio) {
  sex <- rbinom(as.numeric(n), 1, sex_ratio) + 1 # 1=female, 2=male
  return(sex)
}

#'[FUNCTIONS: Convert SVL to TL or vice versa based on sex-specific conversion]
make_TL <- function(size, sex) {
  a_svlTL <- c(2.2390, 2.3121)
  b_svlTL <- c(0.9707, 0.9622)
  TL <- a_svlTL[sex] * (size^b_svlTL[sex])
  return(TL)
}
make_SVL <- function(size, sex) {
  # a & b parameter values from Table 7 Woodward et al. 1992; c(F,M)
  a_svlTL <- c(2.2390, 2.3121)
  b_svlTL <- c(0.9707, 0.9622)
  SVL <- (size/a_svlTL[sex])^(1/b_svlTL[sex])
  return(SVL)
}

#'[FUNCTION: Alligator growth model, Baker-form of Schnute model]
grow <- function(sex, Ym) {
  tau = c(0, 45) # age (yrs) at hatchling and max life expectancy
  deltaT = 1 # duration of growth period
  y1 = 12.5 # SVL at hatching (cm)
  y2 = c(135.9, 186.9) # terminal SVL c(F,M)
  a = c(0.11, 0.09); b = c(0.72, 0.69) # growth rate(a) and shape(b) c(F,M)
  modelErr = c(5.9, 7.42) # model error c(F,M)

  # Compute expected SVL after annual growth, use to draw realized value from
  # normal distribution, then convert to TL if below terminal size for sex;
  # otherwise, keep last TL
  iYr <- (((Ym^b[sex]) * exp(-a[sex]*deltaT)) +
    ((y2[sex]^b[sex]) - (y1^b[sex])*exp(-a[sex]*(tau[2] - tau[1])))) *
    ((1 - exp(-a[sex]*deltaT)) /
    (1 - exp(-a[sex]*(tau[2] - tau[1])))))^(1/b[sex]) %>%
  rtnorm(n = length(.), mean = ., sd = sqrt(modelErr[sex]), lower = Ym)
  newTL <- ifelse(Ym <= y2[sex],
    make_TL(size = iYr, sex = sex),
    make_TL(size = Ym, sex = sex))

  return(round(as.numeric(newTL), 1)) # TL(cm) for t+1
}

#'[FUNCTION: Create initial population, no replicates]
make_founders <- function(N0_k) {
  set.seed(2021)

```

```

# Draw sex variable for each founding population member
p_male <- c(0.5, 0.63, 0.53, 0.53, 0.90) # size class-specific ratio M to F

pop <- map(as.integer(unique(size_class)),
          function(c) tibble(size_class = rep(c, N0_k[c]),
                             sex = assign_sex(n = N0_k[c],
                                                sex_ratio = p_male[c]) %>%
                             as.integer) %>%
          arrange(., sex) %>% mutate(TL = 0))

size_lims <- c(18, 30, 122, 183, 274, 300)

svl_lims <- array(c(size_lims[1:5] %>% make_SVL(size = ., sex = 1),
                  size_lims[2:6] %>% make_SVL(size = ., sex = 1),
                  size_lims[1:5] %>% make_SVL(size = ., sex = 2),
                  size_lims[2:6] %>% make_SVL(size = ., sex = 2)),
                dim = c(5,2,2),
                dimnames = list(c(), c("min", "max"), c("F", "M")))

pop <- map_dfr(seq(pop), function(c) pop[[c]] %>% setDT(.))

pop[, TL:= map2_dbl(pop$sex, pop$size_class,
                  ~ runif(1, min = svl_lims[.y, "min", .x],
                        max = svl_lims[.y, "max", .x]) %>%
                  make_TL(size = ., sex = .x))]

founders <- tibble(sex = pop$sex, TL = pop$TL) %>%
  mutate(z = size_class[TL] %>% factor(., levels = state)) %>%
#size_class[TL]) %>%
  arrange(., desc(z), sex, desc(TL)) %>%
  mutate(t_recruit = as.integer(1), .before = 4) %>%
  mutate(mature = if_else(sex == as.integer(1),
                        as.integer(0),
                        as.integer(NA))) %>%
  mutate(f = as.integer(NA)) %>%
  mutate(ind = as.character(1:sum(N0_k)), .before = 1) %>% setDT
return(founders)
}

#[FUNCTION: ...]
list2cols <- function(x) { x %>% unlist %>%
  matrix(., nrow = n_reps, byrow = TRUE) %>% t() }

#[FUNCTION: ...]
set_quota <- function(harvest_policy, Nh_t, H_max = Qmax) {
  # Harvestable population count (i.e. Nh_t partially observed)
  yNh_t <- rbinom(1, Nh_t, 0.35)

  if (length(harvest_policy) == 2) {
    eta <- 1 / (1 + exp(harvest_policy[1]*(harvest_policy[2] - yNh_t)))
    Q <- round(eta * H_max)
    if (any(yNh_t == 0)) {Q[which(yNh_t == 0)] <- 0}
  }
}

```

```

    return(Q) # total harvest quota
  } else {
    lamdaQ <- rbinom(1, yNh_t, harvest_policy)
    return(lamdaQ)
  }
}

#[FUNCTION: compute density-dependent size-specific annual survival]
dd_phi <- function(adD_0, b_c, phi0, D_t) {
  suppressMessages(map_dfc(D_t, ~
    plogis(q = qlogis(phi0) + (b_c * (log10(.x) -
log10(adD_0)))) %>%
    round(digits = 4) %>% c(., rep(0,4))) %>%
as.matrix() %>% unname)
}

###[FUNCTION: nual survival outside harvest for each i based on z and t(due to dd)
get_phi_it <- function(phi_ct, z_it) {
  phi_it <- phi_ct[as.integer(z_it)]
  return(phi_it)
}

#[FUNCTION: Probability that adult female reaches sexual maturity given TL]
# her_TL=180.5; adult_density=0.193
puberty <- function(her_TL, adD_t = NULL) {
  base_offset <- -(-17.46644/0.087134877) # baseline TL offset for OL (200.4529)
  OL_slope <- 0.087134877 # slope logit(pM) by female TL

  if (is.null(adD_t)) {
    logit_pM <- OL_slope * (her_TL - base_offset)
  } else {
    DD_offset <- base_offset + (b_D * (log10(adD_t) - log10(adD_0)))
    logit_pM <- OL_slope * (her_TL - DD_offset)
  }
  pM <- 1 / (1 + exp(-(logit_pM))) # convert to probability scale
  sexually_mature <- rbinom(length(pM), 1, prob = pM)
  return(sexually_mature)
}

#[FUNCTION: ...]
nesting <- function(N_adFM, save_repro) {
  repro <- imap_dfr(N_adFM, ~ {
    nests <- rbinom(.x, 1, prob = 0.398)
    surviving_nests <- rbinom(nests, 1, prob = 0.452) * nests
    eggs <- rpois(.x, mean_clutch) * surviving_nests
    surviving_eggs <- rbinom(length(eggs), eggs, prob = 0.875)
    repro <- data.table(nests, surviving_nests, eggs,
      surviving_eggs, rep = .y, year = t))
  })
  return(repro$surviving_eggs)
}

#[FUNCTION: make pop_members-like table for new hatchlings to add to survivors of
t, in t+1]

```

```

recruitment <- function(n_recruits, last_id, year_hatched, pop_rep) {
  #'[FUNCTION: for ...]
  f_hatch_TL <- function(n_hatched, sex) {
    svl <- runif(n_hatched,
                min = make_SVL(18,sex),
                max = make_SVL(30,sex))
    hatchling_TLs <- make_TL(size = svl,
                             sex = sex)

    return(hatchling_TLs)
  }
  recruits <- tibble(sex = as.integer(assign_sex(n = n_recruits,
                                                sex_ratio = 0.5)),
                    TL = as.double(f_hatch_TL(n_hatched = n_recruits,
                                              sex = sex)) ,
                    z = factor(as.integer(size_class[TL]), levels = 1:9),
                    t_recruit = rep(as.integer(year_hatched+1),
                                    length = n_recruits),
                    mature = if_else(sex == as.integer(1), as.integer(0),
                                     as.integer(NA)),
                    f = as.integer(NA),
                    rep = pop_rep) %>%
    arrange(., desc(z), sex, desc(TL)) %>%
    add_column(.,
              ind = as.character((last_id+1):(last_id+n_recruits)),
              .before = 1) %>%
    setDT(.)
  return(recruits)
}

#'[FUNCTION: Based on i records for year t, generate i records object for t+1]
year_end <- function(gators_t) {
  # Remove gators that were dead at the beginning of t
  gators_t1 <- gators_t[z != "9", ]

  # Convert state z from factor to integer for ease in next steps
  gators_t1[ , z := as.integer(z)]

  # Harvest recoveries at the beginning of t now dead (for t+1)
  gators_t1[z %in% 6:8, z := 9]

  # Update records for harvested gators
  gators_t1[h == 1, ':= ' (z = z + 3, TL = 0, f = 0)]

  # Update state for gators that died of non-harvest mortality in t
  gators_t1[which(z <= 5 & h == 0 & s == 0), ':= ' (z = 9, TL = 0, f = 0)]

  # Grow surviving individuals
  gators_t1[s == 1, TL := grow(sex = gators_t1[s==1, sex],
                              Ym = make_SVL(size = gators_t1[s==1, TL],
                                              sex = gators_t1[s==1, sex]))]

  # Update state for survivors
  gators_t1[s == 1, z := as.integer(size_class[gators_t1[s == 1, TL])]]
}

```

```

gators_t1[ , z := factor(z, levels = state)]

# Reset fecundity
gators_t1$f <- as.integer(NA)

# Updated records for t+1
updated_gators <- gators_t1[,c("ind", "sex", "TL", "z", "t_recruit",
                               "mature", "f", "rep")]
#return(updated_gators)

pop_t1 <- gators_t[, sum(f, na.rm = TRUE), by = rep] %>% pull(V1) %>%
  imap(., function(n, r) {
    if (n == 0) { updated_gators[rep == r, ]
    } else {
      recruitment(n_recruits = n,
                  last_id = max(as.integer(gators_t[rep == r, ind])),
                  year_hatched = t,
                  pop_rep = r) %>%
      bind_rows(updated_gators[rep == r, ], .)
    }
  }) %>% rbindlist()
return(pop_t1)
}

for (t in tH0:n_years) {

  ## [FALL CENSUS] ----
  pop[ , t, "N", ] <- gators[, summary(z, .drop = FALSE), by = rep] %>%
    pull(V1) %>% list2cols()

  gators[, "t_obs" := t][ , "h" := 0] # add column for year variable

  ## [HARVEST] ----
  if (t < tH0) {

    pop[ , t, "H", ] <- 0

  } else {
    # Based on abundance of sa+, get quota, realize total harvested based on 87.5%
    hunter success rate
    H <- pop[3:5, t, "N", ] %>%
      colSums() %>% as.integer() %>%
      set_quota(harvest_policy, Nh_t = .) %>%
      rbinom(n_reps, ., 0.875)

    taken <- map(seq(n_reps), function(r) {
      sample_size <- min(sum(pop[3:5, t, "N", r]), H[r])
      sample(x = gators[z %in% c(3:5) & rep == r, ind],
            size = sample_size,
            replace = FALSE)})

    if (any(lengths(taken)==0)) {break}
    # ** slow

```

```

# Update individual record
map_df(seq(n_reps), function(r){
  gators[rep == r & ind %in% taken[[r]], h := 1]
})

# If gators taken
if (any(gators$h == 1, na.rm = FALSE)) {

  # Record number harvested by size class
  pop[ , t, "H", ] <- gators[h == 1, summary(z, .drop = FALSE), by = rep] %>%
    pull(V1) %>% list2cols()
} else {
  pop[ , t, "H", ] <- 0
}
}

# Post-harvest adult density
adD_t <- map_dbl(seq(n_reps), ~ pop[4:5, t, c("H","N"), .x] %>%
  colSums %>% diff %>% as.integer(./OL.ha)

## Compute density-dependent survival rates for remainder of the year
pop[ , t, "phi", ] <- dd_phi(adD_0 = adD_0, b_c = b_k, phi0 = phi0, D_t = adD_t)

# ** slow
gators[ , phi_it := map2_dbl(as.integer(gators$z), as.integer(gators$rep),
  ~ { get_phi_it(phi_ct = pop[ , t, "phi", .y], z_it
= .x) })
][h == 1, phi_it := 0
][as.integer(z) <= 5 & h == 0 & (t-t_recruit > 40),
  phi_it := max(0.01, 0.60 - 0.59*((t-t_recruit)-40)/(75-40)), by = "ind"
][, s := rbinom(n = nrow(gators), size = 1,
  prob = gators$phi_it)]

# Mortality count; no. alive at beg. of t, not harvested, but died
pop[ , t, "M", ] <- gators[ , summary(z[TL != 0 & h == 0 & s == 0],
  .drop = FALSE), by = rep] %>%
  pull(V1) %>% list2cols()

pop[ , t, "S", ] <- pop[ , t, "N", ] - pop[ , t, "H", ] - pop[ , t, "M", ]

## [PUBERTY] ----
gators[TL >= 183 & sex == 1 & s == 1 & mature == 0, mature :=
  puberty(her_TL = gators[ , TL[.I[TL >= 183 & sex == 1 & s == 1 & mature
== 0]]),
  adD_t = adD_t[as.integer(gators[ , rep[.I[TL >= 183 & sex == 1 &
s == 1 & mature == 0]]))]]

## [NESTING] ----
gators[s == 1 & mature == 1,
  f := nesting(N_adFM = gators[s==1 & mature==1, .N, by=rep]$N,
  save_repro = save_repro)]

if (save_gators == TRUE & t >= (tH0 - 1)) {

```

```

    save_i_data(data = gators, year = t)
  }

  # ** kinda slow
  ## [RECRUITMENT & GROWTH] ----
  # Update pop records for t+1 and integrate records for new recruits w/
  # existing population members
  if (t < n_years) {
    gators <- year_end(gators_t = gators)
  }

} # close t loop

# Compute total annual harvest
if (t < n_years) {
  utility <- 0
} else {
  H_ts <- map(seq(n_reps), ~ colSums(pop[3:5, 1:n_years, "H", .x], na.rm = TRUE))
  avg_cumH <- map_dbl(H_ts, ~ .x %>% sum()) %>% mean()
  avg_rangeN <- map(seq(n_reps),
    ~ colSums(pop[1:5, 1:n_years, "N", .x], na.rm = TRUE)) %>%
    map_dbl(., ~ max(.x[tH0:n_years]) - min(.x[tH0:n_years])) %>%
    mean()
  utility <- avg_cumH / avg_rangeN
}

# Save replicate population timeseries records
if (!missing(save_pop)) {
  if (!missing(fileID)) {
    filename <- paste0("pop_ts_", thedate, fileID, ".RDS")
  } else {
    filename <- paste0("pop_ts_", thedate, ".RDS")
  }
  saveRDS(pop, file = filename)
}

if (!missing(return_pop)) {
  utility_ts <- list(U = utility, pop = pop)
  return(utility_ts)
} else {
  return(utility)
}

} # close simulate_pop fxn

## code for genetic algorithm

```

```

# Run ga() started 6/13/22 in obelisk screen 0613-----
x_lims <- matrix(c(c(0, 0.07), c(0, 2000), c(100, 1000)), ncol = 2, byrow = TRUE)

sim_pop_before_th0(n_reps = 50, n_years = 101, th0 = 51)

GA <- ga(type = "real-valued", seed = 9999,
         fitness = function(x) {
           sim_pop_from_th0(x = x, save_policy = TRUE,
                             n_reps = 50, n_years = 101, th0 = 51)},
         lower = x_lims[,1], upper = x_lims[,2],
         popSize = 200, maxiter = 100, run = 50, parallel = 20)
saveRDS(GA, file = paste0("GA_", thedate, "_0.RDS"))

summary(GA)

# -- Genetic Algorithm -----
# GA settings:
# Type = real-valued
# Population size = 200
# Number of generations = 100
# Elitism = 10
# Crossover probability = 0.8
# Mutation probability = 0.1
# Search domain =
#   x1 x2 x3
# lower 0.00 0 100
# upper 0.07 2000 1000
#
# GA results:
# Iterations = 96
# Fitness function value = 9.289787
# Solution = x1 x2 x3
# [1,] 0.01077239 451.9207 278.8045

```