FACTORS AFFECTING OUTCOMES OF RECOVERY ACTIONS FOR GOPHER TORTOISES (*GOPHERUS POLYPHEMUS*): CHALLENGES AND OPPORTUNITIES ASSOCIATED WITH HEAD-STARTING AND MAINTAINING OPTIMAL HABITAT

by

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ABSTRACT

Over half of all extant turtle species are listed as threatened by extinction. In addition to being highly sought-after for consumption, medicinal purposes and the pet trade, their habitats are also regularly subjected to fragmentation, degradation, and destruction. Mitigation of these threats often require multi-faceted solutions. This study aimed to supplement a depleted population of gopher tortoises on the 1,894-ha Yuchi Wildlife Management Area in Burke County, Georgia by releasing head-started juveniles reared in captivity. Evaluation of post-release survival of tortoise's head-started for 2.5 and 3.5 years was used to assess survival benefits of longer-term head-starting. Morphometrics and a suite of physiological metrics (*e.g.,* plasma and fecal corticosterone, heterophil:lymphocyte ratios, lactate) were evaluated as potential predictors of post-release movement and survival. Although head-starting can be a beneficial recovery tool, it is recognized that habitat management remains key to successful augmentation efforts yet continues to present challenges to population recovery efforts. Therefore, through semi-structured interviews, several state and federal agency managers' current perceptions and operational restrictions related to the habitat management needs for gopher tortoises were evaluated. Collectively, this research should provide a greater understanding of head-starting as a recovery tool for gopher tortoises and to better understand the limitations and challenges to implementing the on-the-ground habitat management necessary for population persistence.

INDEX WORDS: Population augmentation, head-starting, survivorship, corticosterone, physiological challenges, habitat management, management perceptions

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Globally, turtles are considered among the most threatened of the vertebrate orders with over half of all extant species listed as threatened by extinction (Rhodin *et* al. 2018, Stanford *et al.* 2020). In addition to being highly sought after for consumption (Cheung and Dudgeon 2006, Conway-Gómez 2008), medicinal purposes (Chen *et al.* 2009), and illegal poaching for the pet trade (Mendiratta *et al.* 2017, van Dijk *et al.* 2001), their habitats are also regularly subjected to fragmentation, degradation, pollution and destruction (BenDor *et al.* 2009). In most turtles, life history traits such as delayed sexual maturity, low offspring survival, and low recruitment of reproducing adults can make them especially vulnerable to such anthropogenic perturbations and their populations slow to recover. Therefore, mitigation of these threats often requires multi-faceted conservation approaches (Crawford *et al.* 2020, Spencer *et al*. 2017). Habitat protection and compatible land management are vital aspects in the conservation of all turtle and tortoise species; however, in some cases land stewardship alone is not enough to ensure persistence or aid in recovery. As a result, population augmentation techniques (*e.g.*, wild-to-wild translocations, head-starting) may need to be implemented in addition to land management to recover or bolster populations in decline.

One species of concern that has sparked many conservation initiatives is the gopher tortoise (*Gopherus polyphemus*). The gopher tortoise is a long-lived keystone species found in the southeastern Coastal Plain of the United States (Catano and Stout 2015, Eisenberg 1983).

Tortoises serve as ecosystem engineers due to their ability to dig extensive burrows reaching upwards of 20 m long and 3 m deep (Ashton and Ashton 2008, Catano and Stout 2015). These burrows can provide refuge to nearly 360 other vertebrate and invertebrate commensal species from thermal extremes, predators, and fire (Jackson and Milstrey 1989, Johnston *et al.* 2017). Because tortoises are primarily herbivorous, they are also important agents of seed dispersal and germination (Birkhead *et al.* 2005, MacDonald & Mushinksky 1988).

Although gopher tortoises primarily reside in well-drained, sandy soils with herbaceous ground cover consisting of legumes and forbs, and open canopy, they can persist in a variety of ruderal habitats (Diemer 1986, MacDonald and Mushinsky 1988). The once vast longleaf pine (*Pinus palustris* Mill.)-wiregrass (*Aristida beyrichiana* Trin. and Rupr) ecosystem, which many gopher tortoises inhabit, has declined by more than 98% across its range (Noss *et al*. 1996). Over the last century, gopher tortoise populations have experienced an estimated 80% decline (USFWS 2012), primarily as a result of habitat loss and degradation from encroaching development and fire suppression (Auffenberg & Franz 1982, Diemer 1986). Under the Endangered Species Act, they are federally listed as threatened west of the Tombigbee and Mobile rivers in Alabama to southeastern Louisiana, and are a candidate for federal protection in eastern populations from Georgia to Florida and southeastern South Carolina (USFWS 2011).

Because of their life history traits, gopher tortoises are particularly vulnerable to chronic threats that reduce survival; however, even once threats have been addressed populations can be slow to recover (Tuberville *et al.* 2014). Tortoises can live more than 60 years but don't reach sexual maturity until approximately 10-20+ years of age depending on latitude and resource abundance (Iverson 1980, Epperson and Heise 2003, Landers *et al.* 1982, Rostal and

Jones 2002, Smith 1995, Smith *et al.* 1997). However, tortoises have low offspring survival due to predation of nests and hatchlings (Dziadzio *et al.* 2016, Epperson and Heise 2003, Pike and Seigel 2006). Females lay a single clutch per year, averaging 4-12 eggs per clutch (Ashton *et al.* 2007, Epperson and Heise 2003, Iverson 1980 Landers *et al.* 1980). It is estimated that only 1 out of 100 hatchlings survive to become a reproductive adult (Landers *et al.* 1980). Consequently, population stability is contingent on sustaining high adult and subadult survival, and chronic reductions in this can result in population decline (Congdon *et al.* 1993, Heppell *et al.* 1996). Once the requirement of high adult survivorship is met, population persistence is most sensitive to juvenile survivorship, making it a potential management target (Tuberville *et al.* 2008). By increasing the number of hatchlings surviving to become juveniles, head-starting has the potential to reduce one of the primary bottlenecks to recruitment and ultimately increase the number of reproducing adults on the landscape.

Through input from species biologists, the Gopher Tortoise Council established the following criteria to support a minimum viable population (MVP) of gopher tortoises: at least 250 reproductive adults occurring at a density of ≥0.4 tortoises per hectare and on a site with at least 100 hectares of ideal habitat (Gopher Tortoise Council 2013, 2014). These guidelines are currently being applied across the species' range to identify populations that currently meet MVP criteria, and determine those that need management interventions, such as through augmentation via translocation or head-starting. Some populations may be close enough to meeting MVP criteria that habitat management alone may be able to promote population viability. However, even sites supporting populations that currently meet MVP criteria require frequent application of fire and other management activities. Thus, having established MVP guidelines can also aid agencies when making decisions about resource and conservation effort allocation among populations at specific sites.

For gopher tortoises, fire timing and frequency should mimic historical fire occurrences (Mushinsky 1985, Guyer and Bailey 1993). To produce appropriate foraging (Cox *et al.* 1987, Haywood *et al.* 2001), cover (Kirkmann *et al.* 2001, Means and Campbell 1981) and open canopy (McIntyre *et al.* 2019) associated with high quality gopher tortoise habitat, summer growing season burns are preferred to winter, dormant season burns. In this system, prescribed fire every 1-3 years is required to reduce the abundance of competing hardwoods and other fire-intolerant invasive species and to consume dense leaf-litter accumulation (Glitzenstein *et al.* 2003, Haywood *et al.* 2001, Kirkmann *et al.* 2001, Brockway and Lewis 1997). These habitat management techniques allow for an open canopy that supports the diverse herbaceous ground cover that comprises the bulk of the gopher tortoise's diet, which includes plants of 68 genera from 26 families (Birkhead *et al.* 2005, MacDonald and Mushinsky 1988).

Head-starting as a conservation strategy

Augmenting turtle populations can occur either through translocation or reintroduction programs, such as head-starting (Burke 2015; Tuberville *et al.* 2015). Translocation is the intentional movement of a focal species from one location to another. Head-starting is the practice of rearing a focal species in captivity during early vulnerable life stages to increase survival in the wild. Both translocation and head-starting are used to aid in the improvement of a species' conservation status and restore ecosystems (Burke 2015; Tuberville *et al.* 2015). Tortoises that are displaced from their source location due to development-driven habitat destruction can be used to augment populations at designated recipient sites. These displaced tortoises are often dominated by adults, so translocating them can directly increase the number of adults in recipient populations. Although translocation of displaced wild tortoises has been successfully used to establish new populations or augment depleted populations (Riedl *et al*. 2008, Tuberville *et al.* 2008), the availability of displaced tortoises is unpredictable. Although resulting in a greater time lag before recruitment of reproductive adults, head-starting can provide a more reliable source of animals for release without negatively impacting the source population (Quinn *et al.* 2018). Head-starting allows for a portion of hatchlings from source populations to be released as juveniles to augment depauperate recipient populations. Tortoises may also be well-suited for head-starting as all turtle species are oviparous, or egg laying, with no parental care beyond nest guarding, which has only been documented in very few species (Burke 2015). Turtles reared in captivity also seem to exhibit natural behaviors following their release into the wild (Radzio *et al*. 2019, Tetzlaff *et al.* 2018).

Head-starting is slowly becoming an accepted conservation tool for population recovery in many chelonian species but efforts to date have varied greatly in terms of techniques and overall success (Daly *et al.* 2018, Mitrus 2005, Mullin 2019). One understudied aspect of head-starting turtles is the effect of head-starting duration on physiological health and the resulting implications on post-release performance or behavior. Post-release survival of both wood turtles (*Glyptemys insculpta*) and box turtles (*Terapene carolina carolina*) has been shown to increase with increasing head-starting duration (Mullin 2019, Tetzlaff *et al.* 2019). The pattern of increased survival with longer head-starting duration may be largely due to the additional opportunity for growth. For example, post-release survival increases with increasing size at release in head-started Mojave Desert tortoises (*Gopherus agassizii*) regardless of captive duration and husbandry treatment (McGovern *et al*. 2020). Although captive rearing represents a vital tool of many conservation programs, concerns about head-starting and potential detrimental effects of extended captivity remain.

Early efforts suggest that head-started gopher tortoises may experience higher survival than their same-aged (but smaller) wild counterparts, yet that survival can vary over small temporal and spatial scales (Perez-Heydrich *et al.* 2012, Quinn *et al.* 2018, Tuberville *et al*. 2015). In addition, those early studies lacked an experimental component; however, a recent study demonstrated that head-started yearling gopher tortoises experience approximately 30% higher short-term survival compared to hatchlings released simultaneously at the same site (Tuberville *et al*. 2021). Previous head-starting studies have primarily focused on short term (≤ 1 year) head-starting (Quinn *et al.* 2018, Tuberville *et al.* 2021); however, neither the potential survival benefits nor the potential physiological health costs associated with extended captivity have been evaluated in gopher tortoises. While differences in movement and survival may be due to head-starting methods or release techniques, much of the variation among individuals often remains largely unexplained (Daly *et* al. 2019, Tetzlaff *et al.* 2018, Tuberville *et al.* 2019). Individual-level factors that may help elucidate post-release behavior include personality traits (Allard *et al.* 2019, Germano *et al.* 2017) and measures of physiological status (Fazio *et al.* 2014).

Physiological metrics in head-starting

Chronic physiological challenges can have wide ranging adverse effects on wildlife, including immune suppression, reductions in growth or reproduction, and aberrant behaviors (Blaustein *et al.* 2012, Nacci *et al.* 2001, Cyr and Romero 2007). In wildlife, these challenges can be induced by many different variables, including environmental pollutants (Blanco *et al.* 2004; Maurer and Holt 1996), anthropogenic changes to the landscape (Ditchkoff *et al.* 2006), and even animal conservation programs (*e.g.*, translocation and reintroduction programs; Teixeira *et al.* 2007). The potential for conservation interventions such as translocation, reintroduction, and captive rearing to affect baseline stress-associated hormone levels remains relatively unexplored, as is the role of physiological challenges in influencing the outcomes of those interventions. Capture myopathy—often fatal, stressor-induced muscle degeneration of captured wild animals—accounts for the greatest number of mortalities associated with wildlife translocations (Breed *et al.* 2019); however, many translocation programs are becoming increasingly aware of risks associated with translocation-induced stress or mortality, and are taking the necessary steps to improve conditions for wildlife during captivity (Dickens *et al.* 2010, Landa *et al.* 2017). Substantial methodological improvements to reduce physiological challenges during translocation and reintroduction practices have recently received attention in mammals (Letty *et al.* 2000, Viljoen *et al.* 2008, Wolfe and Miller 2016) and birds (Jenni *et al.* 2015), but has generally been lacking for reptiles. In turtles, researchers are beginning to implement different translocation and reintroduction techniques that could reduce negative physiological challenges and improve post-release success; however, many still do not validate those improved techniques by measuring the physiological response of an individual to that potential stressor. This could be a result of a lack of understanding about stress-associated hormones and the significant role they can play in an individual's survival (Teixeira *et al.* 2007). Likewise, little is known about the effects of extended captivity on the physiological condition of reptiles. With population augmentation programs, such as head-starting, becoming increasingly popular to bolster declining populations, researchers are starting to acknowledge measures of physiological challenges as a vital component of conservation (Drake *et al.* 2012, Kalliokoski *et al.* 2012). It is important to continue research not only to understand whether individuals are adversely affected during these interventions, but also to understand how that physiologic response potentially affects the outcome or success of these programs.

A stressor can be defined as either an internal or external stimulus representing a threat to an individual's homeostasis or survival (Arena and Warwick 1995, Martínez Silvestre 2014, Wingfield *et al.*1998). In reptiles, this stimulus is then regulated through the stimulation of the sympathetic nervous system and the response is activated by the hypothalamus-pituitary-adrenal (HPA) axis (Greenberg and Wingfield 1987, Reeder and Kramer 2005). The hypothalamus secretes a corticotrophin-releasing hormone, which signals the release of adrenocorticotropin hormone (ACTH) into the bloodstream (Axelrod and Reisine 1984, Sheriff *et al*. 2011, Webster Marketon and Glaser 2008). The adrenal gland responds to the presence of ACTH and initiates the synthesis and release of glucocorticoids (Greenberg and Wingfield 1987, Neuman-Lee *et al.* 2020).

One of the most commonly used metrics to measure physiological challenges is the measurement of glucocorticoids. Glucocorticoids are stress-associated hormones used to mitigate an individual's response to threats and to eventually return physiological systems to homeostasis (Sheriff *et al*. 2011). Corticosterone is the primary glucocorticoid in reptiles (Martínez Silvestre 2014) and is often measured in plasma. Plasma corticosterone can increase within minutes of the onset of a stressor (Romero and Reed 2005, Tylan *et al.* 2020), and because plasma corticosterone circulates in the blood stream it increases quickly in response to capture or handling, thus giving a snapshot of the individual's physiological state in that moment (Touma and Palme 2005).

Fecal corticosterone, on the other hand, is considered representative of a more integrated measure of circulating corticosterone rather than an episodic fluctuation (Goymann *et al.* 1999, Harper and Austad 2000, Keay *et al.* 2006, Touma and Palme 2005). This makes the measure of fecal corticosterone less prone to capture as a stressor, particularly if a sample is volunteered or even collected without handling the animal. Thus, fecal corticosterone is more likely to reflect physiological responses resulting from extended captive rearing or chronic disturbances. However, little is known about intestinal transit time in turtles; therefore, it is difficult to determine the precise time frame for which the fecal sample is representative. In mammals, an increase in fecal glucocorticoids reflected physiological challenges experienced anywhere from 6-50 hours before defecation (*e.g.*, 6-12 h in rodents, Harper and Austad 2000; 24-50 h in hyenas, Goymann *et al.* 1999). Regardless, voluntary fecal samples collected incidentally while handling animals can serve as a valuable resource for measuring corticosterone because the samples can be associated with a known animal, sample quality is generally high because they are less prone to environmental contamination if collection occurs shortly after deposition, and samples can often be quickly stored until further analyses (Millspaugh and Washburn 2004). Some studies have demonstrated that mildly invasive research activities (*e.g.,* trapping, handling, blood collection, attachment of radio-transmitter, temporary captivity) do not increase plasma or fecal corticosterone in turtles (Kahn *et al.* 2007; Rittenhouse *et al.* 2005) while others have documented a significant increase in plasma corticosterone in response to capture and handling stressors (Boers *et al.* 2019, Drake *et al.* 2012).

Other metrics can be used to evaluate physiological challenges, as they are positively related to the magnitude of a perceived stressor but can also reveal evidence of disease or infection (Davis *et al.* 2008). The increase of glucocorticoids initiates fluctuations in leukocytes, or white blood cells, by increasing the circulation of heterophils (H) and subsequently suppressing the creation of lymphocytes (L), thereby increasing H:L ratios (Davis *et al.* 2008, Dhabhar *et al.* 1996, Dhabhar 2002). Unlike hormonal responses to physiological challenges, initial leukocyte response times can vary across taxa from hours to sometimes days (*e.g.,* ungulates ~1 h, newts ~3 days, frogs ~12-144 h, fish ~12 h, house finches >1 h, Davis *et al.* 2008). In ectothermic animals (*i.e.*, turtles), the delay in leukocyte response may be attributed to their temperature-dependent metabolism (Pough 1980); this latency can facilitate accurately defining baseline H:L ratios while being less likely to be influenced by physiologic responses to short-term capture or handling (Davis *et al.* 2008, Goessling *et al.* 2015). Unlike plasma corticosterone, H:L ratios have a weak positive correlation with the duration of a stressor and do not appear to attenuate over time (Goessling *et al*. 2015). Chronically elevated glucocorticoids can cause long-term elevation of H:L ratios, making H:L ratios a potentially valuable tool for measuring physiological challenge across a wide variety in both captive and wild settings (Davis *et al.* 2008, Goessling *et al.* 2015). Natural variation in H:L ratios has been linked to disease susceptibility in birds (*e.g.*, poultry, Al-Murrani *et al.* 2006; great tits, Krams *et al*. 2012); thus, H:L ratios have the potential to predict post-release health or survival in translocation and reintroduction programs.

Because reptiles have the ability to support strenuous activity using anerobic metabolism and have unique mechanisms for ridding their systems of lactate, lactate can evaluate physiological challenge in the form of physical exertion (*i.e.*, struggling against restraint during handling; Hamilton 2016, Rosenburg *et al.* 2018). Approximately 50% of lactate is produced within 30 seconds of capture or physical exertion and nearly 90% is formed within the first 90 seconds (Bennett and Licht 1972); therefore, even minimal handling restraint of an animal can quickly result in increased levels. If levels of lactate accumulate over prolonged periods and an individual is unable to metabolize it for oxidation, gluconeogenesis or protein synthesis, lactate has the potential to reach toxic levels causing deleterious effects (Gleeson and Dalessio 1989, Hill 2017, Warren and Jackson 2008).

There are numerous individual metrics that can be used to evaluate physiological responses to environmental stressors but they can sometimes give conflicting results, respond at different rates, or evaluate different aspects of the response. Thus, it may be prudent to use a suite of indices to characterize physiological challenges (Baker *et al.* 2013, Davis and Maney 2018, Palme 2019). If we better understand how pre-release physiological metrics relate to post-release survival and movement, researchers can potentially use preventative measures to lessen mortality and increase site fidelity. For examples, researchers could monitor husbandry techniques or captivity conditions to evaluate the physiological responses of individuals in relation to the controlled environment in which they are being reared in (Harper and Austad 2000). Likewise, if certain individuals are identified as experiencing “physiological challenges” that could increase their post-release movements, release protocols for those individuals could incorporate a soft-release component to facilitate post-release monitoring of their health, encourage acclimation to the release site (Lockwood *et al.* 2005, Tuberville *et al.* 2005), and even provide some measure of protection from predators (Tetzlaff *et al.* 2019, Tetzlaff *et al.* 2020) during the initial exploratory phase when movement tends to be greatest

Management and policy implementation

Historically, wildlife management has primarily relied on biological information when determining conservation actions (Organ *et al.* 2012). However, social science and the role of human dimensions in natural resource management is increasingly used to inform the management of modern conservation challenges that include wildlife governance reform (Rudolph *et al.* 2012), competing public views (*i.e.*, wildlife as a resource for human use vs. wildlife as sentiment; Manfredo *et al.* 2018, Bath 1998), organizational development of natural resource agencies, and conflict resolution (Decker *et al.* 2012, Jacobson and McDuff 1998, Manfredo *et al.* 2019, Moseley and Charnley 2013). More specifically, given the inter- and intra-governmental complexities of many natural resource agencies, it is important to consider several factors in policy implementation that are becoming increasingly recognized as components for understanding and identifying strengths and weaknesses of conservation efforts. These components include different agency organizational structures (*e.g.*, leadership roles and responsibilities, individual expertise and skills), stakeholder preferences, management challenges, best practices in decision-making, agency perceptions and culture, and goal ambiguities (Busenberg 2004, Danter *et al.* 2000, Lind-Riehl *et al.* 2016, Pomeranz *et al.* 2014, Schultz *et al.* 2019). These factors can be especially important when considering the conservation of many endangered or threatened species (*e.g.*, large carnivores, Bruskotter and

Shelby 2010, Way and Bruskotter 2012; RCW, Weiss *et al.* 2019) and the preservation of their respective habitats (Bergles 2006).

Many gopher tortoise populations have experienced significant declines on both private (Hermann *et al.* 2002) and protected (McCoy *et al.* 2006) lands. Management of tortoise-occupied sites, even when maintaining or restoring habitat for gopher tortoises where it is specifically recognized as a desired outcome, can be complicated by several factors: (1) multiple agencies or sectors within an agency with different goals or objectives (Maier and Wirth 2018); (2) the need to manage for multiple uses, including income generation from timber production (Jones and Dorr 2004, Parish *et al*. 2020) or military readiness (Wilson *et al.* 1997); (3) lack of understanding between land managers and scientists regarding the implementation of habitat management (Jacobson *et al.* 2006) for gopher tortoises; and (4) the need to manage for multiple species, such as game species or other at-risk species (*e.g.*, RCW, Tuberville *et al.* 2007).

The U.S. Fish and Wildlife Service (USFWS) developed a Candidate Conservation Agreement (CCA) as a cooperative, range-wide approach for the conservation of gopher tortoises (USFWS 2008). In the state of Georgia, nearly 15 federal, state, non-governmental and private organizations, and agencies are signatories. The agreement includes proactive strategies for conserving gopher tortoises and the management of their respective habitats. It is also designed to serve as tool to increase cooperation and collaboration efforts across and within agencies–which in some cases has proven to be successful. Many federal, state, and non-governmental natural resource agencies have similar goals and initiatives in place for the conservation of species in decline and their respective habitats; yet agency perspectives, decision-making processes, and goal ambiguities on how those efforts should be implemented can vary across and even within agencies (Pomeranz *et al.* 2014, Moseley and Charnley 2013). Both federal (*e.g.*, USFWS) and state natural resource agencies (*e.g.*, Georgia Department of Natural Resources, GADNR) can make management decisions for gopher tortoises at their own discretion. However, there can also be a disconnect within an agency between different resource sectors (*e.g.,* forest management, game management, conservation management; Greene *et al.* 2020, Maier and Wirth 2018, Ascher 2001) with individual actors performing different roles and responsibilities (*e.g.*, Chief, Directors, Program and Regional Managers, Species and Wildlife Biologists, Land Managers, Technicians). Collectively, this can lead to considerable variability in policy implementation at the local scale due to competing interests, performance measurements and differing management goals (Lind-Riehl *et al.* 2016). Often this can result in less than optimal conditions for tortoises, which can contribute to site abandonment by gopher tortoises (Catano *et al*. 2014, Jones and Dorr 2004, McCoy *et al.* 2013) or reduction in tortoise densities to levels where mating opportunities become limited (Guyer *et al.* 2012) and ultimately threaten population viability.

For many species of conservation concern, population declines can be a direct result of the disruption of ecosystem processes, such as habitat loss, fragmentation (BenDor *et al.* 2009), and land use changes (Litvaitis 1993, Northrup *et al*. 2019). However, one disruption of ecosystem processes that is acknowledged, but not commonly evaluated, stems from land management practices or absence of targeted land management, leading to degraded habitat quality. For example, in the southeastern United States' longleaf pine-grassland ecosystems, fire suppression has negatively affected many plant and animal species which are now consequently rare or in decline (Van Lear *et al.* 2005). Some have argued that it is more important to make broader management decisions for an ecosystem rather than species-specific management objectives (Benson *et al.* 2012); however, it has also been shown that temporary single species management can not only directly benefit the species of conservation concern, but indirectly benefit other animals inhabiting surrounding areas under the same management (*e.g.,* RCW, Weiss *et al.* 2019). There is potential for this to be true for the management of gopher tortoise as well. Tortoises will often linger long after habitat becomes unsuitable (McCoy and Mushinsky 1992) and the presence of tortoises on the landscape is often misinterpreted as indicating suitable habitat. Depending on site conditions, if habitat can be restored using tortoise-specific management objectives and tortoises are able to establish stable, minimum viable populations, then species-specific management can gradually be replaced by an ecosystem management approach.

There is a significant lack of knowledge regarding how management decisions for tortoise habitat are being made across agencies and organizations, and to what degree management techniques are being implemented at different sites or organization levels. By incorporating a street-level policy implementation aspect into our research, we anticipate gaining a greater understanding of different perceptions regarding gopher tortoise habitat management, potential restrictions or challenges managers may encounter, as well as how and what role these factors play in tortoise management processes among and within natural resource management agencies across Georgia. Ultimately, this can aid in creating avenues for better communication between species biologists and managers and promote the long-term conservation of gopher tortoises.

Research objectives

Collectively, research suggests that head-starting gopher tortoises could be a potentially useful tool for augmenting gopher tortoise populations, but it is imperative to continue advancing and refining methodologies by better understanding factors that drive post-release fate, as well as increasing overall efficiency. Head-starting, however, needs to be used congruently with quality habitat restoration or maintenance. Identifying barriers to implementing effective habitat management for gopher tortoises will help ensure long-term persistence of tortoises on the landscape. Therefore, the objectives of this research are to:

1. Assess the effects of captivity duration on pre-release measures of physiological challenges of gopher tortoises head-started in captivity for 2.5 and 3.5 years to identify the ideal head-starting duration.
    a. Hypothesis:
        i. Physiological responses would be greater in gopher tortoises reared in captivity for 3.5 years than those reared for 2.5 years.
2. Evaluate the role of release size, captivity duration, and physiological health using a suite of physiological metrics in predicting post-release movement and survivorship.
    a. Hypotheses:
        i. Larger tortoises would have greater post-release movements.
        ii. Tortoises reared in captivity for 3.5 years would have greater post-release movements.
        iii. Tortoises with greater physiological responses to head-starting would exhibit lower survival.

3. Describe and compare perceptions of natural resource managers across and within state and federal agencies, timberland companies, and non-profit organizations regarding habitat management needs of gopher tortoises to identify operational restrictions to implementing management actions that promote ideal tortoise habitat conditions.

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CHAPTER 2

PRE-RELEASE STRESS METRICS IN HEAD-STARTED GOPHER TORTOISES AND RELEATIONSHIP WITH POST-RELEASE MOVEMENT AND FATE

Introduction

Globally, turtles are considered among the most threatened of the vertebrate orders with over half of all extant species listed as threatened by extinction (Rhodin *et* al. 2018, Stanford *et al.* 2020). In addition to being highly sought after for consumption (Cheung *et al.* 2006; Conway-Gómez 2008), medicinal purposes (Chen and Dudgeon 2009), and illegal poaching for the pet trade (Mendiratta *et al.* 2017; van Dijk *et al.* 2001), their habitats are also regularly subjected to fragmentation, degradation, pollution and destruction (BenDor *et al.* 2009). In most turtles, life history traits such as delayed sexual maturity, and low offspring survival can make them especially vulnerable to such anthropogenic perturbations and their populations slow to recover. Therefore, mitigation of these threats often requires multi-faceted conservation approaches (Crawford *et al.* 2020, Spencer *et al*. 2017). Habitat protection and compatible land management are vital aspects in the conservation of all turtle and tortoise species; however, population augmentation techniques (*e.g.*, wild-to-wild translocations, head-starting) may need to be implemented in addition to land management to recover or bolster populations in decline.

Head-starting—the practice of rearing animals in captivity during vulnerable life stages to increase survival in the wild (Frazer 1992; Burke 2015; Tuberville *et al.* 2015)—is an augmentation technique used to help recover populations across many vertebrate taxa (*e.g.*, mangrove finch, Cunningham *et al*. 2015; green iguana; Escobar *et al*. 2010; Tasmanian devil, Rogers *et al.* 2016). Head-starting is becoming an increasingly accepted tool for chelonian conservation (e.g., loggerhead sea turtles, Abalo-Morla *et al*. 2018; Blanding's turtle, Green 2015, Buhlmann *et al*. 2015; wood turtles, Mullin 2019). Thus far, most studies have primarily investigated only short term (≤ 1 year) head-starting, with little attention to the potential survival benefits of longer-term head-starting or any potential negative consequences of extended captivity. It is important to continue optimizing methods of head-starting (*e.g.*, duration of head-starts raised in captivity) to identify and implement the best species-specific practices and increase efficiency of head-starting programs (McGovern *et al.* 2020a, McGovern *et al.* 2020b). Short-term success of head-starting efforts is commonly measured through post-release movement and survivorship (Abalo-Morla *et al.* 2018; Nagy *et al.* 2015; Tetzlaff *et al.* 2019). However, physiological challenges should also be considered as a potential limitation on the success of head-starting and other reintroduction programs (Teixeira *et al.* 2007), especially considering that these measures are largely unexplored as a factor in influencing individual post-release behavior and performance.

Research measuring physiological responses of turtles to mildly invasive or routine research activities (*e.g*., trapping, handling, blood collection, radiotransmitter attachment) as well as to translocation has shown conflicting results (Boers *et al.* 2019, Drake *et al.* 2012, Fazio *et al.* 2014, Kahn *et al.* 2007, Rittenhouse *et al.* 2005). Both mildly invasive research activities and translocation programs may cause short-term physiological challenges to an individual; however, translocation can potentially cause long-term physiological challenges both in response to the translocation itself but also because individuals must adjust to a new environment following release (Fazio *et al.* 2014, Tracy *et al.* 2006). The physiological effects of captive rearing head-started turtles, however, are not well investigated. Further, evaluating pre-release stress-associated hormones has the benefit of informing researchers of the overall health of individuals (Martínez Silvestre 2014, Rosenberg *et al.* 2018)—information which can in turn be used to optimize the quality of animals used to augment populations. Much like differences of individual personalities, pre-release measures of physiological challenges also have the potential to predict behavioral responses (Germano *et al.* 2017, Pusch *et al.* 2018) in turtles after introduction into the wild (Allard *et al.* 2019).

A stressor can be defined as either an internal or external stimulus representing a threat to an individual's homeostasis or survival (Arena and Warwick 1995, Martínez Silvestre 2014, Wingfield *et al.*1998). Different physiological indices commonly used to evaluate physiological challenge exhibit different latencies between when a perceived stressor occurs and when a measurable alteration can be detected. Therefore, to thoroughly investigate physiological challenges in head-started animals, studies should consider a suite of metrics rather than a single physiological measure (Goessling *et al.* 2015, MacDougall-Shackleton *et al.* 2019), including plasma and fecal glucocorticoids, heterophil to lymphocyte (H:L) ratios, and lactate. An increase release of corticosterone, the primary glucocorticoid or stress-associated hormone in reptiles, can be detected as a response to stressful stimuli (Martínez Silvestre 2014). Plasma corticosterone can be measured to quantify circulating corticosterone in blood. It can increase within approximately three minutes of handling or capture (Baxter-Gilbert *et al.* 2014, Boers *et al.* 2019, Gregory *et al.* 1996, Romero and Reed 2005, Tylan *et al.* 2020); however, it can also attenuate in the continued presence of a stressor (Goessling *et al*. 2015). Fecal corticosterone is non-invasive and can often be collected opportunistically or with minimal disturbance; therefore, it may give a more accurate representation of circulating corticosterone over the time frame during which a potential stressor (*i.e.*, living in captivity) occurred (Harper and Austad 2000, Keay *et al*. 2006) without being influenced by stress due to capture or handling. Leukocyte, or white blood cell, profiles such as H:L ratios can also be used to evaluate physiological challenges, as they are positively related to the magnitude of a perceived stressor but can also reveal evidence of diseases or infection (Davis *et al.* 2008). With the onset of a perceived stressor, circulation of heterophils increase and the creation of lymphocytes decrease, resulting in elevated H:L ratios (Dhabhar *et al.* 1996, Dhabhar 2002). Unlike hormonal responses to physiological challenges, initial leukocyte responses can vary across taxa from hours to sometimes days (*e.g.,* house finches >1 h, ungulates ~1 h, fish ~12 h, frogs ~12-144 h, newts ~3 days, Davis *et al.* 2008). The leukocyte response in ectothermic animals, such as turtles, is typically delayed due to their temperature-dependent metabolism (Pough 1980). Therefore, this latency can facilitate accurately defining baseline H:L ratios while being less likely to be influenced by physiologic responses from short-term capture or handling (Davis *et al.* 2008, Goessling *et al.* 2015). Unlike plasma corticosterone, H:L ratios have a weak positive correlation with the duration of a stressor and do not appear to attenuate over time (Goessling *et al*. 2015). Finally, lactate has been used to evaluate physiological challenges in the form of physical exertion and can rapidly increase within minutes of an animal being handled or restrained (Bennett and Licht 1972). Thus, each metric provides different insight into the physiological state of an individual organism.

Over the last century, gopher tortoise (*Gopherus polyphemus*) populations have experienced an estimated 80% decline (USFWS 2012) as a result of habitat loss and degradation. Currently, they are federally listed as threatened west of the Tombigbee and Mobile rivers in Alabama to southeastern Louisiana and are a candidate for federal protection in eastern populations from Georgia to Florida and southeastern South Carolina (USFWS 2011). Only a few studies have investigated the potential utility of head-starting gopher tortoises, but collectively these studies have demonstrated that head-started gopher tortoises can exhibit high post-release survival (Quinn *et al.* 2018, Tuberville *et al*. 2015, Tuberville *et al.* 2021), presumably due to increased size at release (Tuberville *et al*. *In press*). Tortoises head-started for nine months averaged an annual survivorship of 70% post-release (Quinn *et al.* 2018) which is >4 times greater than the estimated 12.8% annual survivorship of wild hatchlings (Perez-Heydrich *et al.* 2012). However, minimal research has evaluated survival of gopher tortoises head started for ≥1 year, as well as if there are any negative physiological consequences of extended captivity. Additionally, if a suite of pre-release metrics used to evaluate an individual's physiologic status proves useful in predicting post-release movement and survivorship of head-started tortoises, it could allow researchers to manage conservation efforts more effectively by potentially modifying husbandry practices to reduce negative physiological implications or adapt release and monitoring protocols to increase the chances of survival once released into the wild (Dickens *et al.* 2010, Teixeira *et al.* 2007). This could also facilitate the adoption of better management decisions on the forefront, rather than waiting to determine fate following release.

This study aims to use a suite of pre-release physiological metrics (*i.e.,* plasma and fecal corticosterone, H:L ratios, lactate) to evaluate whether physiologic status differs between gopher tortoises head-started for 2.5 and 3.5 years. Furthermore, the study aims to determine whether any pre-release physiological metrics predict post-release movement of individual turtles and whether those movements in turn influences whether or not they survived their first year following release. Therefore, the objectives of this research are to:

4. Assess the effects of captivity duration on pre-release measures of physiological challenges of gopher tortoises head-started in captivity for 2.5 and 3.5 years to identify the ideal head-starting duration.
    a. Hypothesis:
        i. Physiological responses would be greater in gopher tortoises reared in captivity for 3.5 years than those reared for 2.5 years.
5. Evaluate the role of release size, captivity duration, and physiological health using a suite of physiological metrics in predicting post-release movement and survivorship.
    a. Hypotheses:
        i. Larger tortoises would have greater post-release movements.
        ii. Tortoises reared in captivity for 3.5 years would have greater post-release movements.
        iii. Tortoises with greater physiological responses to head-starting would exhibit lower survival.

Methods

Study Site and Study Population

Yuchi Wildlife Management Area (YWMA) is a 3,100-ha protected area of the Upper Coastal Plain near Waynesboro, Georgia (Burke County). In 1988, Georgia Department of Natural Resources (GADNR) acquired the property from Kimberly-Clark Corporation, a forest products company. At the time of acquisition, the tract was planted with primarily slash (*Pinus elliotti*) and loblolly (*P. taeda*) pine. Since then, GADNR has made efforts to replant longleaf pine (*P. palustris*) to restore the site back to the longleaf-wiregrass-scrub oak community (GADNR 1994), resulting in 1894 ha of potentially suitable gopher tortoise habitat. The site includes a mixture of upland habitats on deep, well-drained sandy soils (*e.g.*, Lakeland, Troup, Bonifay, Orangeburg, Lucy) suitable for burrowing by tortoises, and gradually transitions into lowland, poorly-drained floodplain soils (*e.g.*, Osier, Chastain, Shell bluff) adjacent to the Savannah River (GADNR 1994). Vegetation structure varies across the upland habitats, which although considered *potentially* suitable for gopher tortoises, consist of a patchwork of suitable and currently unsuitable habitat. The unsuitable upland habitats include mixed pine-hardwood forest of upland pines (*Pinus* spp.) canopy with a heavy scrub-oak (*Quercus* spp.) component midstory, or densely planted pines with a minimal grass-forb component. Groundcover in these unsuitable patches consists primarily of dense patches of wild blackberry (*Rubus* spp.) with little to no wiregrass (*Aristida* spp.), sparse native grasses, forbs or legumes (*i.e.*, Poaceae, Asteraceae, Fabaceae) and some eastern prickly pear (*Opuntia humifusa*). Suitable habitat consists primarily of either early successional planted pine forests or mature forests with a sparse canopy of longleaf pines and hardwoods, and includes some residual wiregrass, wild blueberry (*Vaccinium* spp.), blackberry, forbs, and legumes. Habitat suitability of individual patches changes quickly without frequent management with prescribed fire or other disturbance.

The YWMA is considered a high-priority site for gopher tortoise conservation by GADNR and has been identified as one of the target populations for ensuring representation of gopher tortoises within this ecoregion of the gopher tortoise's range in Georgia (*i.e.*, Conservation Unit GA_3; Gopher Tortoise Council 2013, 2014). In 2007-2008, 2.7% of the habitat potentially suitable for gopher tortoises (based on soil type) was surveyed, and despite habitat restoration efforts by GADNR the population at YWMA remained depleted (Smith *et al*. 2009). Researchers failed to detect any gopher tortoises and found only a few adult burrows, suggesting a small remnant population. Subsequent transect surveys by GADNR detected 27 tortoises. The small size of the resident population at YWMA and concurrent conservation efforts for gopher tortoises on adjacent lands associated with Plant Vogtle prompted GADNR to designate YWMA as a recipient site for displaced wild tortoises (Bauder *et al.* 2014) and head-started gopher tortoises (Quinn *et al.* 2018, Tuberville *et al.* 2021). The Orianne Society translocated 18 adult tortoises to YWMA in 2012 and GADNR translocated an additional 19 adult tortoises in 2013 (Bauder *et al.* 2014; GADNR, unpublished data). Collectively, surveys of resident tortoises and translocations of additional tortoises resulted in an estimated population size of 81 adults and subadults but with no observations of juveniles or hatchlings. In 2014-2016, the University of Georgia's Savannah River Ecology Laboratory (SREL) partnered with GADNR to augment gopher tortoise populations at YWMA through the release of 204 head-started tortoises and to monitor their fate following release (Quinn *et al.* 2018, Tuberville *et al.* 2021). In Fall 2018, SREL released an additional 10 tortoises head-started for two years and two tortoises head-started for three years (Russell *et al.* unpublished data). All prior releases occurred in suitable habitat in the same approximate 70-ha area used in the current study.

Obtaining hatchlings and head-starting husbandry

The 2015 (n=15) and 2016 (n=9) cohorts of tortoise hatchlings were obtained from three donor sites in Georgia (St. Catherine's Island, Liberty County; Reed Bingham State Park, Cook County; YWMA) and head-started indoors for 3.5 or 2.5 years, respectively, until Spring 2019. They were held in a temperature regulated greenhouse, at approximately 25-27 °C, at SREL. Depending on tortoise size and cohort (hatch year), 5-10 tortoises were assigned per rearing bin, which consisted of an oval 190 L Rubbermaid® tub (Newell Rubbermaid, Atlanta, Georgia, USA) with approximately 3 cm of sterile QUIKRETE® Premium Play Sand® (The QUIKRETE Companies, Atlanta, Georgia, USA). Bins included at least 1-2 artificial hide structures (10.2 cm diameter black plastic corrugated tubing cut horizontally into ~15.2 cm halfpipe sections) and an 11.3 L Rubbermaid® Roughneck Storage tote used as a humid hide box filled with saturated PREMIER® Sphagnum Peat Moss (PREMIER TECH Horticulture, Olds, Alberta, Canada) to improve humidity conditions thought to aide in hydration and prevent shell pyramiding in captive-reared tortoises (Wiesner and Iben 2003). Lights were suspended approximately 25 cm over each bin and automatically programmed with a 100 w Zoo Med® PowerSun mercury vapor UVB-UVA bulb (Zoo Med Laboratories Inc., San Luis Obispo, California USA) during the day (0700-1900 h) and a 50 w Exoterra® Infrared Basking Spot (Rolf C. Hagen Group, Montreal, Canada, USA) at night (2000-0600 h) to provide heat. Three times a week, tortoises were soaked for hydration and fed a variety of commercially available greens (Quinn 2016). The combination of greens varied on a weekly basis due to availability and seasonality but always consisted of a minimum of three different types, including dandelion (*Taraxacum officinale*), mustard greens (*Brassica juncea*), turnip greens (*Brassica rapa*), collards (a cultivar of *Brassica oleracea*), endive (*Cichorium endivia*), and escarole (*C. endivia latifolia*). Greens were sprinkled with Fluker's® Calcium:Phosphorus 2:1 (Fluker Farms, Port Allen, Louisiana, USA) to promote shell hardness, and moistened Mazuri® Tortoise Diet (Mazuri Exotic Animal Nutrition, St. Louis, Missouri, USA) to approximate the nutrient content of their natural diet.

Morphometrics and body condition

Each individual was uniquely and permanently marked by filing notches on marginal scutes (Appendix A, modification of Cagle 1939). Mass (to nearest 1 g), midline carapace length (MCL, to nearest 1 mm), maximum shell width, and maximum shell height were recorded on 9 April 2019, the day prior to release. Morphometrics were used to calculate body condition based on the formula described by Nagy *et al.* (2002):

$$Body\ condition\ \left(\frac{g}{cm^3}\right) = \frac{weight\ (g)}{shell\ volume\ (cm^3)}$$

$$Shell\ volume\ (cm^3) = MCL\ (cm) * width\ (cm) * height\ (cm)$$

Pre-release visual health assessments were also performed to determine presence or absence of and to describe any externally visible abnormalities (e.g., eyes, nares, respiration, musculature, skin, shell deformities, etc.; see Appendix A). All animal handling procedures conformed to Animal Use Proposal #A2017 05-022-Y1-A0 approved by UGA's IACUC and Scientific Collecting Permit Number #1000540516 from Georgia Department of Natural Resources.

Pre-release physiological metrics

On 7-8 April 2019, biological samples (*i.e.*, blood and feces) were collected to quantify a suite of metrics to characterize pre-release physiological responses (*i.e.*, at time of release) of head-started gopher tortoises. To minimize effects of handling on pre-release metrics, tortoises were not fed, soaked, or disturbed for a minimum of 24 hours prior to sample collection. The suite of metrics used to assess physiological condition included lactate levels, H:L ratios, and plasma and fecal corticosterone.

No more than 0.5 mL of blood for every 100 g of tortoise mass was collected from the subcarapacial venous sinus (Hernandez-Divers *et al*. 2002). Approximately 95 uL of whole blood was immediately analyzed for lactate using a point-of-care VetScan iSTAT Analyzer (CLEW A37, Abaxis, Union City, California, USA) and an iSTAT CG4+ cartridge (Abaxis, Union City, California, USA). A minimum of three blood smear slides were created and subsequently inspected by a certified clinical pathologist (Dr. Nicole Stacy, University of Florida), who blindly evaluated smears for white blood cell estimates, white blood cell differentials (200 cells), and blood cell morphology. Heterophil:lymphocyte ratios were calculated by dividing the total number of heterophil cells by the total number of lymphocyte cells out of the first 200 cells observed and averaged across blood smear slides. Approximately 75 uL of whole blood was placed in a microhematocrit tube and centrifuged to determine packed cell volume (PCV), quantifying red blood cell percentage. Total protein was determined using a refractometer (Reichert Technologies, Depew, NY, USA) to determine total protein (TP) of the blood sample. Both PCV and TP were used as a means of detecting poor sample quality due to lymph contamination, or potential anemia or dehydration of individual animals (Boyer 1998). The remaining whole blood was centrifuged to separate red blood cells from plasma, which was then partitioned into multiple 110 uL aliquots and frozen at -70 °C until further analysis. Any fecal samples voided by tortoises were collected, placed in whirl-paks (Nasco Sampling/ Whirl-pak®, Madison, Wisconsin, USA), labeled according to individual and time of sample collection, and stored at -70 °C for later analysis.

Corticosterone was extracted from 50 ul plasma samples (n=25) using diethyl ether and then quantified with a colorimetric competitive enzyme-link immunosorbent assay (ELISA) kit (ADI-900-097; Enzo Life Sciences, Incorporated, Farmingdale, New York, USA). ELISA kit instructions were followed, and all standards and samples were run in duplicate. After accounting for sample recovery (96% in this study), final plasma corticosterone concentrations were determined.

Fecal samples (n=22) were freeze dried for 48 hours to a constant mass and homogenized using a mortar and pestle. To minimize the chances of cross-contamination, the mortar and pestle were cleaned with ethanol between samples. Corticosterone was extracted from approximately 50 mg of dried fecal sample in 90% ethanol for two hours. A double antibody radioimmunoassay (RIA) kit (SKU 07120102; MP Biomedicals, LLC, Solon, Ohio, USA) was then used to measure fecal corticosterone. RIA kit instructions were followed, and all standards and samples were run in duplicate. Fecal corticosterone concentrations were quantified on the RiaCalc WIZ gamma counter (Wallac 1470 Wizard®, Software version 3.6, PerkinElmer™, Wallac Oy, Waltham, Massachusetts, USA).

Releases and post-release monitoring

On 9 April 2019, 13-mo radio-transmitters (Advance Telemetry Systems Model R1680, 3.6 g, Isanti, Minnesota, USA) were attached to the left or right posterior carapace using J-B WELD® WaterWeld™ Epoxy Adhesive (J-B WELD®, Sulphur Springs, Texas, USA). The weight of the radio-transmitter and epoxy accounted for no more than 5% of pre-attachment body mass at release. On 10 April 2019, 25 individuals were released at abandoned adult gopher tortoise burrows on YWMA during 1100-1400 hrs. Twenty-four were released in pairs, and an additional individual was released by itself. Tortoises were radio-tracked at 24 h and 48 h after release, then tracked every other day for the first two weeks. Thereafter, tortoises were tracked twice a week during the active season until winter dormancy (15 November 2019). At each tracking event, the following data were recorded: time and date the tortoise was found, the tortoise's location to nearest ± 3 m using a handheld GPS (GARMIN® GPSMAP® 76CSx, Olathe, Kansas, USA), burrow ID (if applicable), distance from last known location (m), cover or shelter type (*e.g.*, burrow, apron, pallet, open, shrub, clump grass, leaf litter, course woody debris), and tortoise activity (*e.g.*, basking, digging, foraging, interacting, resting, walking).

To quantify post-release movement and behavior, the following movement metrics were calculated for each individual from their tracking history: maximum distance moved between any two sequential tracking events, mean distance moved per tracking event, days to establish first burrow following release, and final displacement from release burrow. For those individuals who were known to survive until winter dormancy (defined in this study as 15 November, following Quinn *et al.* 2018), their winter dormancy burrow was used as their final location. For those animals that died or went missing, their final location was the last location at which they were last observed alive. Distance metrics were calculated using the Spherical Law of Cosines (Movable Type Ltd. 2015). Surface activity, burrow switching, and fate (dead, alive, or unknown) were also determined. Surface activity was calculated as the number of times a tortoise was found outside of a burrow divided by the total number of tracking events. Burrow switching was defined as the number of unique burrows used by an individual divided by the number of tracking event that individual was found in a burrow.

If a tortoise was found deceased, the surrounding area and carcass were thoroughly examined for evidence of cause of death. The carcass was photographed as found and brought to SREL for further analysis. Death was attributed to either coyote predation, raccoon predation, unidentified predator, or exposure. “Coyote predation” was assigned when remains of shell were gnawed, chewed, had obvious tooth marks, or was found scattered in many pieces where the mortality event occurred. “Raccoon predation” was assigned when the legs, head, or body of tortoise looked to be pulled out and only the shell remained. “Unidentified predator” was assigned when a definitive assessment between coyote or raccoon predation could not be made. If a tortoise was found intact and dead on the surface or inside a burrow, the mortality event was presumed to occur due to “exposure.” There were no suspected mortalities due to fire ants (*Solenopsis invicta*). Fate of each individual was determined at end of study (15 Nov 2019) as alive, dead, or unknown. An “unknown fate” classification was given to a tortoise if it was lost due to a faulty radio-transmitter (*i.e.*, failing transmitter batteries or antenna damage).

Statistical methods

Data are reported as group means ± 1 standard error (SE). All statistical analyses were performed using Program R (R Core Team 2019), and all inferences were supported at a threshold type I error rate (alpha) of 0.05. Data were first graphically visualized; Shapiro-Wilk tests were used to check model assumptions of normally distributed residuals. When necessary, data were transformed to meet model assumptions.

An ANOVA was used to determine whether release size (MCL) significantly differed between the two treatment groups (2.5 yr olds vs. 3.5 yr olds). Because 3.5 yr olds were significantly larger than 2.5 yr olds, as expected, subsequent comparisons to test for treatment-level differences in the following pre-release physiological metrics were analyzed using a separate analysis of covariance (ANCOVAs) for each of the following physiological metrics, with MCL as a covariate: body condition, plasma corticosterone, fecal corticosterone, H:L ratios, and lactate.

Because physiological condition might in turn be expected to influence individual behavior or survival, a series of candidate generalized linear models (GLM; 'glm' function) were used to determine if any pre-release physiological metrics (predictor variables) predicted post-release movement metrics or individual fate (response variables). Pairwise comparisons of individual predictor variables were first made to determine if any individual physiological variables were correlated and to avoid multicollinearity in subsequent candidate and fate models. Treatment and MCL were not included as predictors in the same model.

Response variables included both continuous and discrete data. Discrete response variables (days to establish burrow after release, surface activity and burrow switching) were considered count data, and treated as number of successes out of the number of trials in GLMs with family = 'binomial' and link = 'logit' using the 'cbind' function. Continuous outcome variables (maximum distance moved, mean distance moved, final displacement) were run as GLMs with family = 'gaussian,' and link = 'identity.' Coefficients of the binomial GLMs were also exponentiated to interpret results as incident rate ratios. For each post-release response variable, we constructed a series of 10 candidate models (Appendix A) that included a null model, size or treatment group (based on 'duration in captivity' alone), each pre-release physiological metric alone, and additive models with size or treatment group in combination with a single physiological metric. Due to limited sample size, no interactions were considered. Akaike's Information Criteria (AIC) was used to compare candidate models within the model set. The model with the lowest AIC was deemed the best fit model; however, all models with a ΔAIC < 2 of the best fit model were considered supported. For each supported model, significant predictors were identified. These results were used to prioritize the movement metrics to be considered as predictors in subsequent fate analysis. Because movement metrics are likely to be influenced by the duration over which the animal was tracked, the distance from release site was plotted against days since release for each individual to identify the time period at which dispersal from release site reached a clear asymptote. As shown in Figure 2.1, the displacement asymptote was determined to be 14 days post-release (24 April 2019); thus only individuals that survived at least 14 days post-release were included in fate analyses.

The fate analysis was conducted as a series of GLMs to determine whether treatment (captivity duration) or MCL – alone or in combination with any post-release movement or behavior predictor – can predict post-release fate of head-started gopher tortoises. This analysis did not include any tortoises with unknown fate (n = 3) or individuals that died within 14 days post-release (24 April 2019; n = 2); therefore, only 20 tortoises were included in fate models. Fate was a binary response variable (0 = dead, 1 = alive) based on whether the individual survived until winter dormancy (15 Nov 2019). Treatment and size were included in models, but not in the same model since MCL differed significantly between treatments. Post-release movement and behavior metrics included as predictor variables were maximum distance moved (m), mean distance moved (m), final displacement from release location (m), surface activity, and days to establish first burrow. Because surface activity and days to establish burrow are used as predictor variables in fate models, they were no longer considered count data. Therefore, surface activity was expressed as a proportion and days to establish burrow was simply the number of days it took an individual to dig a burrow. A set of 28 candidate models (Appendix B) was constructed to include a null model, size (MCL) or treatment group (duration in captivity) alone, each post-release movement metric alone, additive models with either size or treatment group in combination with a single post-release movement metric, and models that included an interaction terms between either size or treatment group in combination with a single post-release movement metric. Akaike's Information Criteria (AIC) was used to compare candidate models within the model set. The model with the lowest AIC was deemed the best fit model; however, all models with a ΔAIC < 2 of the best fit model were considered supported.

Results

Morphometric and physiological metrics: treatment comparisons

The two treatment groups overlapped broadly in MCL, but 3.5 yr olds were significantly larger than 2.5 yr olds at release (Figure 2.1.A, ANOVA: $F_{1,23} = 9.593$, $p = 0.005$). Mean release MCL was 136.6 ± 5.9 mm (range: 98.7 – 173.0 mm) for 3.5 yr olds and 110.1 ± 5.5 mm (range: 87.8 – 137.7 mm) for 2.5 yr olds. Mean mass exhibited a similar pattern, with 3.5 yr old head-started tortoises being significantly heavier (522.8 ± 56.1 g; range: 194 – 964 g) than 2.5 yr olds (274.4 ± 42.5 g, range: 122 – 514 g; Figure 2.1.B, ANOVA: $F_{1,23} = 9.223$, $p = 0.006$). Body condition was also significantly greater in 3.5 yr olds than 2.5 yr olds (Figure 2.1.C; ANCOVA: $F_{2,22} = 7.895$, $p = 0.003$) and MCL was a significant covariate ($p = 0.001$)**.** Mean body condition was 0.55 ± 0.01 g/cm^3 (range: 0.49 – 0.58 g/cm^3) for 2.5 yr olds and 0.57 ± 0.01 g/cm^3 (range: 0.50 – 0.65 g/cm^3) for 3.5 yr olds.

Both plasma (0.07 – 1.63 ng/ml) and fecal corticosterone (1.28 – 67.05 pg/mg) varied widely among individuals but neither differed significantly between treatments (Table 2.1; log plasma cort, ANCOVA: $F_{2,22} = 1.421$, $p = 0.263$; log fecal cort, ANCOVA: $F_{2,19} = 1.937$, $p = 0.172$). Heterophil:lymphocyte ratios also were not significantly different between treatment groups (Table 2.1; ANCOVA: $F_{2,22} = 2.661$, $p = 0.092$). For 8 of 25 (32%) of individuals tested, lactate was below the instrument detection limits (< 0.3 mmol/L); values for these individuals were conservatively set at 0.3 mmol/L. Lactate did not differ significantly between treatments (Table 2.1, 1/x transformed, ANCOVA: $F_{2,22} = 0.680$, $p = 0.517$).

Movement metrics: treatment comparisons

Overall, tortoises moved an average of 51.1 ± 7.5 m (n = 25, range: 3 – 123 m) between tracking events with a maximum distance of 142.9 ± 38 m (n = 25, range: 3 – 949 m) between any two tracking events. Final displacement of gopher tortoises from their release location averaged 143.8 ± 27.5 m (n = 25; range: 6.9 – 579.3 m). It took tortoises an average of 15 days (n = 22, mean: 15.4 ± 5.25 days, range: 1 – 103 days) to establish their first burrow following release. The proportion of tracking events during which tortoises were active on the surface averaged 0.2 ± 0.03 (n = 22, range = 0.0 – 1.0) among all released tortoises with a known fate at the end of the study. The proportion of tracking events where tortoises switched between unique burrows over the monitoring period (10 April – 17 November 2019), or until the animal died, averaged 0.18 ± 0.04 (n=22, range = 0 – 0.67). Based on separate ANCOVAs with MCL as a covariate, the only post-release movement metric that was significantly different between 2.5 and 3.5 yr olds was final displacement (Figure 2.2; $F_{2,22} = 6.199$, $p = 0.007$). The 2.5 yr olds moved significantly shorter distances (125.5 ± 37.5 m, range: 14.5 – 343.2 m) than 3.5 yr old head-starts (154.1 ± 38.0 m, range: 6.9 – 579.3 m) and size was a significant covariate ($p = 0.002$). No other movement metric differed significantly between the two treatments (all $p > 0.05$; Table 2.2).

Pre-release physiological metrics as predictors of post-release movement

For each post-release movement response variable, a series of 10 candidate models were used to determine which pre-release physiological metrics best predicted post-release movement in head-started gopher tortoises. For response variables, the top ranked candidate models consistently included fecal corticosterone alone or in combination with duration in captivity (Table 2.3; see Appendix A for list of all candidate models). For maximum distance moved, mean distance moved, and final displacement from release, the most parsimonious model included only fecal corticosterone. Although the fecal corticosterone + duration in captivity model was also supported, fecal corticosterone was the only significant predictor of maximum distance moved or final displacement distance, with distance increasing with increasing fecal corticosterone. For every 1 pg/mg increase in fecal corticosterone, maximum distanced moved increased by 5 m (estimate: 5.144 m, $p < 0.001$) and final displacement increased by nearly 7 m (estimate: 6.927, $p = 0.005$). Neither fecal corticosterone nor duration in captivity was a significant predictor of mean distance moved even though they were included in the top models. Models revealed that it took 2.5 yr olds significantly fewer days to establish a first burrow following release than 3.5 yr olds ($p = 0.006$), and that greater fecal corticosterone concentrations were associated with fewer days to establish a burrow ($p < 0.001$). The 2.5 yr olds exhibited significantly higher surface activity than 3.5 yr olds ($p < 0.001$); for every 1 pg/mg increase in fecal corticosterone, the proportion of surface activity increased by 0.02 ($p = 0.009$).

Predictors of post-release fate

Out of 28 models, the most parsimonious model predicting post-release fate was MCL + Final displacement (weight = 0.21). Three additional models were within $\Delta AIC \leq 2$ of the top model: Duration in captivity x Mean distance moved, MCL x Final displacement, and MCL + Mean distance moved. No model for fate had > 0.25 of AIC model weight indicating high uncertainty in model selection (see Appendix Table B for complete list of models). Across the four top models, only Final Displacement ($p = 0.044$) was considered a significant predictor of fate and only in the top model (MCL + Final Displacement, $\Delta AIC = 0$, Weight = 0.21); as final displacement increased by 1 m the chances of survival decreased by 0.02.

Discussion

All morphometric measurements, including MCL, mass and body condition, were significantly greater in tortoises head-started for 3.5 years than for those head-started for 2.5 years. Gopher tortoises head-started for 8 – 9 months have been shown to grow the size of 2 – 3 yr old wild juveniles (Quinn *et al.* 2018, Tuberville *et al.*2015). In comparison, tortoises head-started for 2.5 and 3.5 years had an average MCL relative in size to 4 – 6 yr old wild juvenile tortoises and 5 – 9 yr old wild juvenile and subadult tortoises, respectively (Aresco and Guyer 1999, Smith 1995). Although there was some overlap between the two treatment groups, the 3.5 yr old tortoises were greater in size likely as a result of active growth during the dormant season and the extended duration in captivity (Mullin 2019). A body condition index based on morphometric data has been used as a tool to access malnutrition, stress, and overall health of individual tortoises (Cozad 2018, Nagy *et al.* 2002, Quinn 2016, Riedl *et al.* 2008). Individuals head-started for 2.5 and 3.5 years exhibited mean body conditions similar to both wild adult male gopher tortoises (Riedl *et al.* 2008) and gopher tortoises head-started for 8 – 9 months (Quinn 2016). Collectively, this suggests that head-starting gopher tortoises for extended durations in captivity do not negatively affect individual growth or nourishment and reflect body conditions of wild counterparts. This could be a result of head-started tortoises, whether for eight months or 3.5 years, being provided with ample nutritional (*i.e.,* leafy greens, calcium powder, tortoise pellets) and environmental (*i.e.,* humidity hide boxes heat lamps, basking hides) resources to successfully thrive in a temporary captive environment. Additionally, results suggest that body condition of head-started gopher tortoises may be independent of age and body size (Nagy *et al.* 2002); however, this merits further investigation of body condition indices of free-living tortoises from different stage classes.

Among the suite of physiological metrics taken, there were no significant differences between treatment groups. In comparison to previous research, one study measured baseline plasma corticosterone of wild adult tortoises' hand-captured at a mean of 1.4 ng/ml (Table 2.4, Ott *et al.* 2000). Baseline plasma corticosterone measured in wild adult tortoises in traps for ≤ 12 hours, which was classified as a time threshold of no physiological response to being captured, had an approximate mean of 7 ng/ml (Table 2.4; Kahn *et al.* 2007, Ott *et al.* 2000). Results suggest that wild tortoises were potentially experiencing a physiological response to being captured in a trap. Lower plasma corticosterone concentrations in the current study could be a result of head-started individuals not being exposed to stressors they might experience in the wild, such as predator-prey interactions, foraging, or unpredictable seasonal changes. Although corticosterone has been found to be significantly elevated in captive populations over wild populations (Goessling *et al.* 2015), captive reared animals can become acclimated to routine handling. There is potential that the tortoises in this study became somewhat acclimated to handling throughout their duration in captivity. When first entering room where tortoises were held, some tortoises would hurriedly move towards their food plate, others would seek immediate shelter in humidity hide boxes, and others wouldn't react at all. Although not significantly different between treatments, fecal corticosterone did vary widely among individuals within each treatment group. The pre-release mean H:L ratio fell within values previously reported (Table 2.5) for wild and captive reared tortoises. Lactate data in the present study were lower than those reported in other chelonians (*e.g.,* loggerhead sea turtles, Harms *et al.* 2003; Galapagos green turtles, Lewbart *et al.* 2014). However, there are no known studies that have explored determining reference intervals for lactate in wild gopher tortoises and only one study that assessed captive tortoises (Rosenberg *et al.* 2018). Gopher tortoises that were temporarily held in captivity (approximately a year) for treatment of medical conditions had lower lactate concentrations (0.4 mmol/L) than tortoises in this study (0.69 ± 0.07 mmol/L). Rosenberg *et al.* (2018) acknowledge that these study animals were habituated to being handled; however, that does not completely explain the difference between the two study groups.

Tortoises in this study moved more than twice the average distance between tracking events of tortoises head-started for 8 – 9 months (Quinn *et al.* 2018); however, average final displacement fell within the maximum displacement range of wild adult tortoises (79 – 189 m; Bauder *et al.* 2014). Final displacement was the only movement metric that was statistically significant between 2.5 and 3.5 yr old tortoises; larger tortoises moved greater distances from release locations. Tortoises head-started for 3.5 years were larger in size, and previous studies have shown that larger tortoises will typically move greater distances than hatchlings or yearlings (Bauder *et al.* 2014, Butler *et al.* 1995. Pike 2006). Similarly, the proportion of surface activity was less than both hatchling and yearling (69.5% and 32.6%, respectively, Pike and Grosse 2006; vs. 20%, this study). This is presumably due to smaller tortoises needing ample energy to achieve high growth rates (Mushinsky *et al.* 2003).

Fecal corticosterone and duration in captivity were consistently the only and best variables to predict post-release movements. Pre-release fecal corticosterone was the only significant predictor of maximum distance moved and final displacement from release location.

Greater concentrations of fecal corticosterone resulted in longer distances moved. Duration in captivity and fecal corticosterone were both significant predictors of days to establish first burrow and surface activity. Shorter durations in captivity and greater fecal corticosterone concentrations resulted in tortoises taking fewer days to establish their first burrow following release. Additionally, younger tortoises and individuals with greater fecal corticosterone concentrations, spent more time on the surface. Collectively, fecal corticosterone could be an opportunity for researchers to use voluntary fecal samples as a non-invasive tool to further evaluate different methodologies and release protocols.

Movement metrics are often a large determinant for the success or failure of introducing captive animals into the wild. How much an animal disperses post-release affects its resource availability and chance of encountering predators, which can influence an individual's chance of survival. Approximately 44% of 2.5 yr olds and 38% of 3.5 yr olds survived to the beginning of winter dormancy (15 Nov). The most parsimonious model predicting fate was MCL + Final displacement with only final displacement as a significant variable. Naïve tortoises dispersing from their release burrows were likely learning the landscape and searching the area to construct a burrow or to find nearby food resources; therefore, as tortoises moved farther away from release burrows their chances of survival decreased.

Conclusions

Collectively, this research suggests that increased duration of captivity does not negatively influence physiological responses in head-started gopher tortoises. However, individuals—regardless of captivity duration—can vary in their physiological state at the time of release. Of the metrics evaluated, fecal corticosterone was the best predictor of post-release movement and fate at the end of the study. Therefore, fecal corticosterone could serve as a biomarker or non-invasive tool to further evaluate different methodologies and release protocols. This would not only be beneficial for introducing head-started tortoises into the wild but for translocation purposes, as well. For example, if an individual has a high fecal corticosterone concentration prior to release indicating potential for greater movements (increasing chances of a mortality event), a soft release can be implemented at a recipient site to allow for acclimation, rather than hard release to increase its chances of survival.

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Tables and Figures

Table 2.1. Pre-release physiological metrics from head-started gopher tortoises (*Gopherus polyphemus*) reared in captivity for 2.5 or 3.5 years. Table terms include MCL (midline carapace length, an indicator of size), plasma cort (ng/ml, plasma corticosterone), fecal cort (pg/mg, fecal corticosterone), H:L ratios (heterophil:lymphocyte ratios), and lactate (mmol/L). An ANCOVA (Analysis of covariance) with MCL (midline carapace length, an indicator of size) as a covariate was used to compare plasma corticosterone, fecal corticosterone, H:L ratios, and lactate between two treatment groups. Table term MCL? answers the question of whether MCL was a significant covariate. Raw values of mean and range reported in tables; plasma and fecal corticosterone were log transformed and lactate was inverse transformed in analyses.

Physiological metric	Treatment	n	Mean	SE	Range	F-value, df, p-value	MCL?
log Plasma cort *(ng/ml)*	2.5	9	0.59	0.15	0.17 - 1.63	1.421, 2, 0.263	No
	3.5	16	0.4	0.09	0.07 - 1.17		
log Fecal cort *(pg/mg)*	2.5	6	10.66	2.44	4.93 - 20.85	1.937, 2, 0.172	No
	3.5	16	15.52	3.66	1.28 - 67.05		
H:L ratios	2.5	9	1.48	0.11	1.11 - 2	2.661, 2, 0.092	No
	3.5	16	1.21	0.08	0.67 - 1.85		
1 / Lactate *(mmol/L)*	2.5	9	0.76	0.25	0.3 - 2.66	0.680, 2, 0.517	No
	3.5	16	0.52	0.09	0.3 - 1.5		

Table 2.2. Post-release movement metrics of head-started gopher tortoises (*Gopherus polyphemus*) reared in captivity for 2.5 or 3.5 years that were released at Yuchi Wildlife Management Area, Burke County, Georgia, USA in April 2019. Table terms include MCL (midline carapace length in mm at release), Duration in captivity (2.5 or 3.5 years), Max dist (m, maximum distance moved between tracking events), Mean dist (m, mean distance moved per tracking event), Final displ. (m, final distance from release location until the animal died, went missing, or until the onset of winter dormancy, or 15 November), Days estab B (days to establish first burrow following release), SA (surface activity, or the proportion of tracking evens that an individual was on the surface), and BS (burrow switching, which is number of unique burrows used by an individual divided by the number of tracking event that individual was found in a burrow). An ANCOVA (Analysis of covariance) with MCL (midline carapace length, an indicator of size) as a covariate was used to compare post-release movement metrics between two treatment groups. Table term MCL? answers the question of whether MCL was a significant covariate. Raw values of mean and range reported in tables; maximum distance, mean distance, days to establish burrow, and burrow switching were log transformed in analyses. Statistically significant physiological measurements ($p \leq 0.05$) are denoted with *.

Movement metric	Treatment	n	Mean	SE	Range	F-value, df, p-value	MCL?
log Max dist *(m)*	2.5	9	84.44	16.25	19 - 150	0.624, 2, 0.545	No
	3.5	16	175.81	57.79	3 - 949		
log Mean dist *(m)*	2.5	9	45.57	12.5	11 - 123	0.761, 2, 0.479	No
	3.5	16	54.21	9.57	3 - 108		
Final displ* *(m)*	2.5	9	125.52	37.49	14.5 - 343.2	6.199, 2, 0.007	Yes
	3.5	16	154.12	38.01	6.9 - 579.3		
log Days estab B	2.5	8	21	12.29	1 - 103	0.248, 2, 0.783	No
	3.5	14	12.14	4.63	1 - 65		
SA	2.5	9	0.3	0.1	0.01 - 1	2.44, 2, 0.113	No

	3.5	13	0.12	0.03	0 - 0.33		
log BS	2.5	9	0.13	0.04	0 - 0.43	0.190, 2, 0.829	No
	3.5	13	0.21	0.05	0.03 - 0.67		

Table 2.3. Top ranked candidate models used to evaluate pre-release predictors (*e.g.*, plasma & fecal corticosterone, heterophil:lymphocyte ratios, lactate, duration in captivity) of post-release movement metrics in gopher tortoises (*Gopherus polyphemus*, n = 23) head-started for 2.5 or 3.5 years that were released at Yuchi Wildlife Management Area, Burke County, Georgia, USA in April 2019. The model with the lowest AIC is the most parsimonious and is indicated by a ΔAIC = 0; however, all models with an ΔAIC < 2 were considered supported and are listed below. Post-release movement metrics are indicated in bold and the top ranked pre-release predictors are listed below. Statistically significant (p ≤ 0.05) predictors are denoted by a *. The only pre-release predictors included in the top ranked models are fecal corticosterone (Fecal cort) and duration in captivity (2.5 or 3.5 years). Post-release movement metrics consist of both continuous and discrete data. Continuous outcome variables include maximum distance moved (between tracking events), mean distance moved (per tracking event), and final displacement from release location (until the animal died, went missing, or until the onset of winter dormancy; 15 November). Discrete, count variables include days to establish first burrow (following release), surface activity (number of times a tortoise was found outside of a burrow divided by the total number of tracking events), burrow switching (number of unique burrows used by an individual divided by the number of tracking event that individual was found in a burrow). Values presented include model degrees of freedom (K), Akaike Information Criteria (AIC), delta AIC (ΔAIC), and Akaike weight (Weight), which displays the weight of each model in the candidate set. Reference Appendix Table 2.1 for all candidate model sets.

Model	K	AIC	ΔAIC	Weight
Maximum distance moved (m)				
Fecal cort*	3	230.471	0	0.645
Duration in captivity + Fecal cort*	4	231.667	1.2	0.355
Mean distance moved (m)				
Fecal cort	3	203.803	0	0.659
Duration in captivity + Fecal cort	4	205.118	1.3	0.341
Final displacement from release location (m)				
Fecal cort*	3	252.565	0	0.724
Duration in captivity + Fecal cort*	4	254.492	1.9	0.276
Days to establish first burrow				
Duration in captivity* + Fecal cort*	3	307.650	0	0.954
Surface activity				
Duration in captivity* + Fecal cort*	3	139.088	0	0.999
Burrow Switching				
Duration in captivity + Fecal cort	3	104.202	0	0.595
Fecal cort	2	105.003	0.80	0.399

Table 2.4. Range and average pre-release plasma corticosterone (ng/ml) concentrations for head-started gopher tortoises (*Gopherus polyphemus*) compared to values reported for gopher tortoises from previous studies. This study reports data as range and mean ± 1 SE, other citations report data as mean ± 1 SD or range.

Citation	Blood collection occurred at:	n	Plasma corticosterone (ng/ml)
This study	Baseline	25	0.07 – 1.63 0.468 ± 0.08
Ott *et al*. 2000	Baseline (opportunistically hand-capturing)	4	1.14 ± 0.25
	Retained in trap for 12 hours	4	7.2 ± 2.90
Kahn *et al*. 2007*	Baseline (>12 hours in trap)	11	7.1 ± 1.80
	8 hours post-manipulation	11	4.9[a]
	30 days post 2nd trapping (>12 hours)	10	8.23 ± 1.50

[a]SE was not reported

Table 2.5. Range and average of pre-release heterophil:lymphocyte (H:L) ratios for head-started gopher tortoises (*Gopherus polyphemus*) compared to values reported for gopher tortoises from previous studies. This study reports data as range and mean ± 1 SE, other citations report data as mean ± 1 SD or range.

Citation	Population characteristics	H:L ratios
This study	2.5 & 3.5 yr old head-starts; GA	0.67 – 2.00 1.30 ± 0.07
McKee, unpublished data	Translocated waifs; SC (AGTP)	1.34 ± 0.81
Holbrook 2015	*In situ* wild; MS (Hillsdale)	1.15 ± 0.87
Holbrook 2015	*In situ* wild; MS (T44)	2.08 ± 1.31
Cozad, unpublished data	Translocated wild; FL	1.98 ± 0.96
Rosenberg *et al.* 2018	Short-term captivity for treatment of medical conditions; FL[a]	Juv. 0.25 – 3.56[b] Adlt. 0.32 – 2.88[b]

[a] H:L ratios determined after medical condition treated and tortoise considered healthy
[b] Reference intervals for juvenile (Juv.) and adult (Adlt.) tortoises calculated using logarithmic transformations, as original data were non-normal

Table 2.6. Range and average of pre-release lactate (mmol/L) for head-started gopher tortoises (*Gopherus polyphemus*) compared to values reported for gopher tortoises from a previous study. This study reports data as range and mean ± 1 SE, other citations report data as mean ± 1 SD or range.

Citation	Population characteristics	Lactate (mmol/L)
This study	2.5 & 3.5 yr old head-starts; GA	0.30 – 2.66 0.69 ± 0.07
Rosenberg *et al.* 2018*	Short-term captivity for treatment of medical conditions; FL[a, b]	0.4

[a] SD was not reported
[b] H:L ratios determined after medical condition treated and tortoise considered healthy

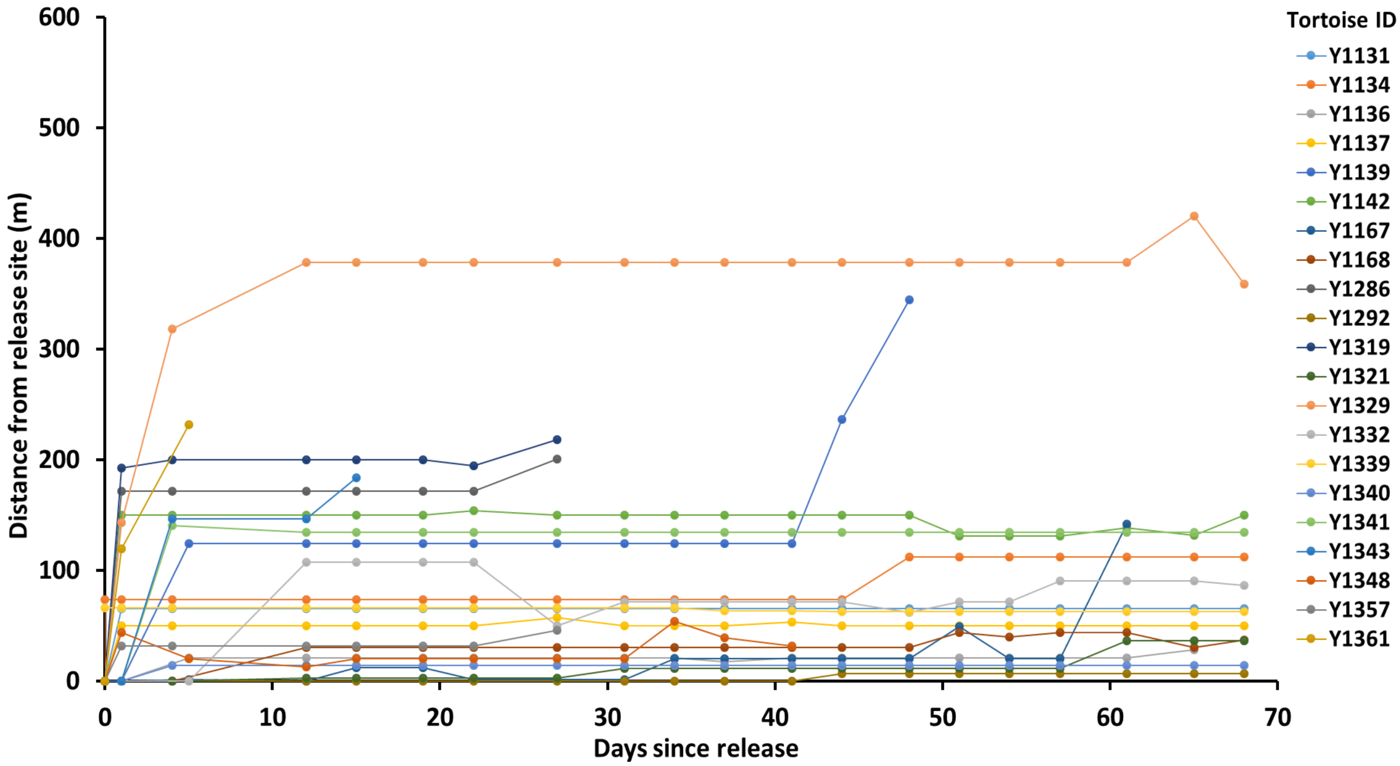

Figure 2.1. Distances moved (m) by head-started gopher tortoises (*Gopherus polyphemus*) from release sites at Yuchi Wildlife Management Area in Burke County, Georgia, USA. Tortoises (n=25) were released on 24 April 2019 and tracked until the onset of winter dormancy (15 November 2019). Figure is trimmed down to 70 days to adequately determine an asymptote for displacement post-release, and includes 24 of 25 tortoises because one individual moved approximately a kilometer away into a wetland and had to be relocated to its original release location. This movement trajectory determined a 14-day post-release asymptote for displacement.

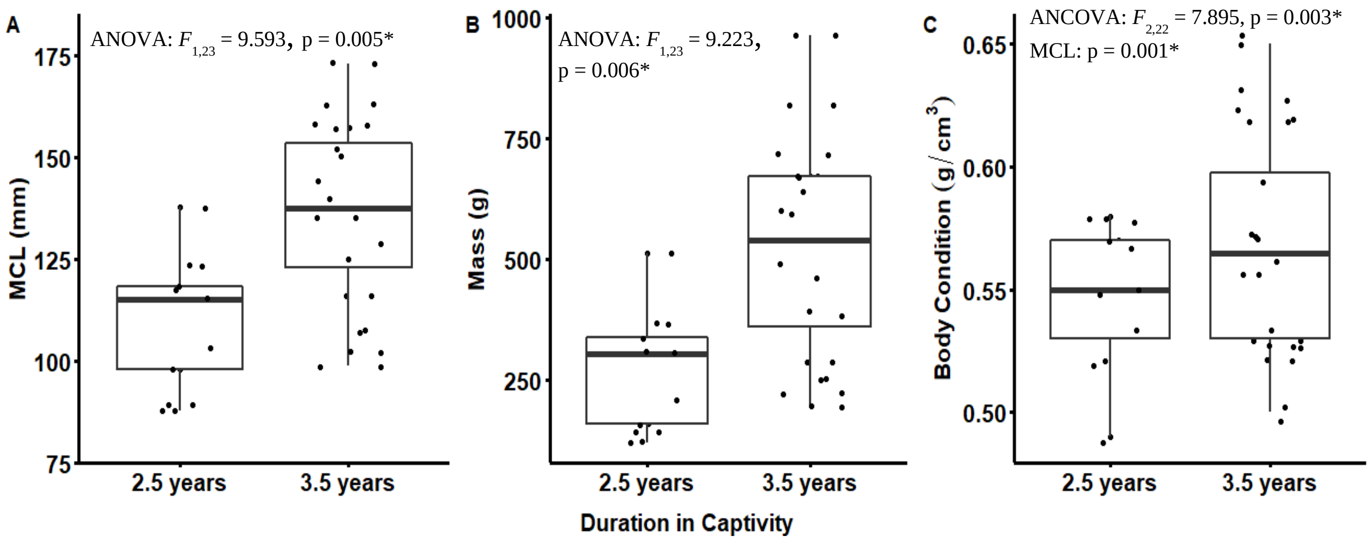

Figure 2.2. Boxplots of pre-release morphometrics and body condition from head-started gopher tortoises (*Gopherus polyphemus*) reared in captivity for 2.5 or 3.5 years. Figure terms include pre-release MCL (mm, midline carapace length), Mass (g), and Body condition (g/cm^3). An ANOVA (Analysis of variance) was used to analyze MCL (A; $F_{1,23}$ = 9.593, p = 0.005) and mass (B; $F_{1,23}$ = 9.223, p = 0.006) between treatment groups; while an ANCOVA (Analysis of covariance) with MCL as a covariate was used to compare body condition (C; $F_{2,22}$ = 7.895, p = 0.003, MCL: p = 0.001) between treatment groups. Statistically significant (p ≤ 0.05) differences between treatment groups (2.5 or 3.5 years) are denoted by a *.

CHAPTER 3

DETERMING PERCEPTIONS AND OPERATIONAL RESTRICTIONS ON GOPHER TORTOISE HABITAT MANAGEMENT

Introduction

Governmental agencies are required by the Endangered Species Act (ESA) to develop strategic plans for increasing populations and reducing threats of many imperiled species (Foin *et al.* 1998); yet these species often occur across landscapes of different ownership types (*i.e.,* federal, state, non-governmental, private) with multiple land management goals and objectives. Historically, wildlife management has primarily relied on biological information when determining conservation actions (Organ *et al.* 2012). However, for conservation efforts to be effective across land ownership types and large spatial scales, it is important to incorporate social science and the role of human dimensions. Natural resource management that incorporates social science can more thoroughly examine different agency organizational structures, stakeholder preferences, management challenges, best practices in decision-making, agency perceptions and culture, and goal ambiguities (Busenberg 2004, Danter *et al.* 2000, Lind-Riehl *et al.* 2016, Pomeranz *et al.* 2014, Schultz *et al.* 2019). These factors are becoming increasingly recognized as important for identifying strengths and weaknesses of conservation efforts for many at-risk species (*e.g.*, large carnivores, Bruskotter and Shelby 2010, Way and Bruskotter 2012; red-cockaded woodpeckers, RCW, Weiss *et al.* 2019) and the preservation of their respective habitats (Bergles 2006).

The gopher tortoise (*Gopherus polyphemus*) is a long-lived keystone species found in the southeastern Coastal Plain of the United States (Catano and Stout 2015, Eisenberg 1983). Under the ESA, they are federally listed as threatened west of the Tombigbee and Mobile rivers in Alabama to southeastern Louisiana, and are a candidate for federal protection in eastern populations from Georgia to Florida and southeastern South Carolina (USFWS 2011). Over the last century, gopher tortoise populations have experienced an estimated 80% decline (USFWS 2012), primarily as a result of the habitat loss and degradation from encroaching development and fire suppression (Auffenberg and Franz 1982, Diemer 1986). Although gopher tortoises primarily reside in well-drained, sandy soils with herbaceous ground and open canopy, they can persist in a variety of ruderal habitats (Diemer 1986, MacDonald and Mushinsky 1988). The once vast longleaf pine (*Pinus palustris* Mill.)-wiregrass (*Aristida beyrichiana* Trin. and Rupr) ecosystem, which many gopher tortoises inhabit, has declined by more than 98% across its range (Noss *et al*. 1996).

Many gopher tortoise populations have experienced significant declines on both private (Hermann *et al.* 2002) and protected (McCoy *et al.* 2006) lands. Management of tortoise occupied sites, even when maintaining or restoring habitat for gopher tortoises where it is specifically recognized as a desired outcome, can be complicated by several factors: (1) multiple agencies or sectors within an agency with different goals or objectives (Maier and Wirth 2018); (2) the need to manage for multiple uses, including military readiness (Wilson *et al.* 1997) or income generation from timber production (Jones and Dorr 2004, Parish *et al*. 2020); (3) a lack of knowledge or clarity among practitioners regarding the ideal habitat conditions for gopher tortoises and the best methods to achieve those conditions; and (4) the need to manage for multiple species, such as game species or other at-risk species (*e.g.*, RCW, Tuberville *et al.* 2007).

The U.S. Fish and Wildlife Service (USFWS) developed a Candidate Conservation Agreement (CCA) as a cooperative, range-wide approach for the conservation of gopher tortoises (USFWS 2008). In the state of Georgia, there are nearly 15 federal, state, non-governmental and private organizations, and agencies that are signatories. The agreement includes proactive strategies for conserving gopher tortoises and the management of their respective habitats. Many federal, state, and non-governmental organizations often have similar goals and initiatives in place for the conservation of declining species and their respective habitats; yet agency perspectives, decision-making processes, and goal ambiguities on how those efforts should be implemented can vary across organizations (Pomeranz *et al.* 2014, Shultz *et al.* 2019). Even within a single organization, there can also be a disconnect between different resource sectors (*e.g.,* forest management, game management, conservation management; Greene *et al.* 2020, Maier and Wirth 2018, Ascher 2001) with individual actors performing different roles and responsibilities (*e.g.*, Chief, Directors, Program and Regional Managers, Species and Wildlife Biologists, Land Managers, Technicians). Collectively, this can lead to considerable variability in policy implementation at the local scale due to competing interests, performance measurements and differing management goals (Lind-Riehl *et al.* 2016).

There is a significant lack of knowledge regarding how management decisions for tortoise habitat are being made across agencies and organizations, and to what degree management techniques are being implemented at different sites or organization levels. Therefore, the aim of this study was to gain a greater understanding of different gopher tortoise management perceptions, potential restrictions or challenges managers may encounter, as well as how and what role these factors play in tortoise management processes among and within natural resource management agencies across Georgia. Ultimately, this could aid in creating avenues for better communication between species biologists and managers and promote the long-term conservation of gopher tortoises.

Methods

From Spring to Fall 2020, semi-structured interviews (n = 27) were conducted via telephone. Recruited interview participants included personnel from state and federal agencies, timberland companies, and non-profit organizations (or non-governmental organizations, NGOs) throughout the gopher tortoise's range in Georgia. Where possible, research participants consisted of natural resource professionals at multiple levels within the hierarchy of an agency or organization and in different professional roles, including land managers, wildlife biologists, herpetologists, and program directors. Interviews covered the following topics: "Professional role and experience," "Habitat management perceptions," "Decision-making, planning and the implementation of habitat management," "Performance measures of habitat management success," and "Looking forward." Interview procedures and questionnaire (see Appendix 3.1) were approved by the University of Georgia's Human Subjects Office (Institutional Review Board proposal approval: PROJECT00001820, 16 March 2020).

Interviews were designed to elicit participants' perceptions of habitat management needs of gopher tortoises, methods for promoting ideal habitat, and potential operational restrictions to implementing appropriate land management actions. Interviewees were recruited to participate in the interview based on their expertise and experience with the subject matter. Interviews generally lasted approximately one hour but interview duration depended on interviewee responses. Additional contact was occasionally requested weeks or months after the initial interview to clarify information, as needed.

All interviews were recorded and transcribed verbatim. Interview transcripts were then coded using Dedoose software (Dedoose, Manhattan Beach, California, USA) to facilitate qualitative data analysis. An inductive process of thematic coding was used to identify emergent patterns across and within organizations. The codebook (see Appendix 3.2) was created and refined as a means of building a consistent analytic approach for linking interview findings to research questions. Codes (n = 61, see Appendix 3.2 for codebook) are representative of the key emergent themes regarding perceptions of gopher tortoise habitat, how tat habitat should be managed, best working practices based on each organization's land management objectives, and operational restrictions to implementing effective management. The ultimate goal of this process was to illuminate the means by which management of gopher tortoise habitat occurs across multiple ownership categories. Using interviewee professional role categories, we also generated simple frequency statistics to show the percentage of interviewees that mentioned particular codes across organizations. Because we did not select a random sample, these frequencies are not intended to represent inferences to larger populations; rather, they are presented as a means of exploring patterns of difference across interviewee categories.

Results

Interviewees consisted of natural resource professionals from federal (n = 7), state (n = 10), NGO (n = 7) and private (n = 3) management agencies (Table 3.1) working throughout the gopher tortoise's range in Georgia. Most of interviewees had extensive experience managing gopher tortoise habitat, with 74% having at least a decade of experience and a third having two or more decades (Table 3.1).

Habitat management perceptions

Ideal versus current gopher tortoise habitat

Throughout interviews, most participants described ideal gopher tortoise habitat to consist of relatively open canopy, xeric soils, and diverse herbaceous ground cover. However, when prompted to discuss current condition of tortoise-occupied habitats he natural resource professionals were managing, interviewees generally indicated that the sites they managed were not representative of the ideal conditions they described. One state interviewee summarized the problem:

> *It's well understood and accepted that habitat loss is the main driver of declines for gopher tortoises, but I think the second factor would be a lack of management. As far as state-owned properties, we have done well in the past, especially this past 5 years to acquire new property… for the management of gopher tortoises. A lot of that habitat still can't support tortoises because of the state it's in… you just don't have the ecosystem and the resources available for gopher tortoises, and they end up being pushed out of those systems.*

Habitat management strategies

Across interviews, there was consistency in strategies identified as tools for managing tortoise habitat including prescribed fire, mechanical treatments (*e.g.*, stand thinning or harvest, roller chopping, etc.), planting (*e.g.*, trees, native ground cover, grasses), and chemical treatments (*e.g.*, use of herbicides). These strategies were broadly reported as a means of increasing the establishment of grasses and forbs, reducing woody species in the midstory, and opening the canopy to better resemble historical longleaf pine ecosystem structure. Although the desire to achieve this habitat structure was described across agencies, participants whose main objective was timber revenue (primarily private timberland interviewees) reported engaging in these practices less often and with the main intent of reducing competition for pine seedlings and reducing woody species in the midstory. It is important to mention that those same participants greatly valued providing suitable habitat for gopher tortoises for as long as possible, but ultimately in a way that is conducive to maximizing their profit margins from harvesting timber.

Prescribed fire was mentioned by all (100%, n = 27, Table 3.2) interviewees as an important practice to manage gopher tortoise habitat. Frequency and seasonality of conducting prescribed burns were primarily emphasized as site-dependent factors based on fuel type, load and continuity, or based on other land management objectives (*e.g.*, other target species, hunting, timber harvest). In general, participants believed that fire contributed to broader goals beyond managing habitat primarily for gopher tortoises. Fire was considered to play an integral role in not only restoring and maintaining pine ecosystems, but managing timber for harvest, reducing detrimental impacts of wildfire, improving aesthetics of properties for outdoor recreational use by the public, as well as benefiting numerous game, non-game and plant species.

Because participants had different educational focuses (*e.g.*, wildlife vs. forestry), workforce experiences, and were operating under a span of differing land use objectives, there were divergent opinions on how, when and why mechanical management techniques (*e.g.*, timber harvest or thinning, roller chopping, site prep, etc.) should be implemented. Overall, however, mechanical management was thought to both improve gopher tortoise habitat and promote broader habitat management goals – with nearly 89% (n = 24, Table 3.2) of participants mentioning such techniques. Some participants acknowledged the potential for mechanical techniques to disturb tortoise burrows or native ground cover, but it was recognized that these techniques were necessary to open canopy cover to increase sunlight on the ground floor and to aggressively attack invasive plants that have created understory or midstory monocultures (*e.g.*, hardwoods, saw palmetto, etc.).

Planting and chemical management techniques were mentioned by the majority of participants (74.1%, n = 20 and 63%, n = 17, respectively; Table 3.2). Planting native grasses was discussed as a means to increase or restore the herbaceous diversity and ground cover gopher tortoises need to thrive. Across agencies, planting longleaf pines was discussed as an important practice to restore longleaf pine ecosystems. Most participants indicated the desire to convert previously planted stands of faster growing, short lived pines (*e.g.*, loblolly pine, *Pinus taeda*; slash pine, *Pinus elliottii*) to longleaf pine. Other participants whose primary objectives were related to timber production revealed that restoring longleaf pines was not economically feasible across all properties. Chemical management, or the application of herbicide, was reported across agencies to control invasive plants such as kudzu (*Pueraria montana*) and cogon grass (*Imperata cylindrica*), or other woody species found dominating the under- or mid-story. This was an important aspect to restoring gopher tortoise habitat that had little to no prior management, but many participants described it as a technique that should be chemical-specific for the targeted invasive species, used in sparing quantities and only implemented once, maybe twice, ever in a single area.

Barriers and challenges to habitat management

When asked about barriers and challenges of decision-making and the implementation of habitat management for gopher tortoises, a pattern emerged with nearly 78% of all participants (77.8%, n = 21, Table 3.3) identifying persistent obstacles to effective gopher tortoise habitat management; collectively, these are referred to as "operational restrictions." Through iterative coding and analysis of the data, the five primary operational restrictions identified were: limitations to applying prescribed fire, conflicting intra-agency views, lack of capacity, time lag, and private landowner distrust and lack of information. Each of these operational restrictions is examined in detail below.

<u>Limitations to applying prescribed fire</u>

Limitations to applying prescribed fire was the most common operational restriction discussed (66.7%, n = 18, Table 3.3). Included among these were temporal or spatial factors related to the inability to burn, smoke management issues, or the inability to acquire sufficient liability insurance. All three private-sector interviewees (100%, Table 3.3) mentioned limitations to applying fire. This was primarily due to private organizations being hindered by contractors unable to carry sufficient liability insurance necessary for the acreage that needed to be burned. Federal and state participants shared similar experiences:

> *So those weather restrictions put a damper on being able to keep up with that 3-year cycle. Sometimes It's a smoke restriction that gets in the way, if the wind just doesn't go the right direction, you've got steady winds coming from a certain direction for weeks at*

a time, and you're like "I need to burn this area," and it just doesn't ever happen. You've got to put it on the back burner and get a dormant season [burn] on it the next dormant season. Sometimes these areas go for 3 to 5 years, 6 years between burning for one restriction or another. –Federal interviewee

Lack of capacity

Lack of capacity was discussed as an operational restriction by nearly 60% of participants (59.3%, n = 16, Table 3.3). Lack of capacity referred to statements made about the inadequacy or inability to execute habitat management needs effectively and efficiently due to not having sufficient personnel or funding. Although some participants from all categories of interviewees, had similar views, this sentiment was expressed by the majority of state interviewees:

…it takes a lot of manpower to manage over 400,000 acres of land out there, especially for gopher tortoises. The minute you start doing things to it like burning, midstory hardwood control, moving understory pines…that's where the challenge comes in. –State agency interviewee

Over 70% of NGO participants (71.4%, n = 5, Table 3.3) mentioned lack of capacity as a challenge to small, private landowners being able to afford gopher tortoise habitat management, sharing:

Realistically, given there are some 900 species of plants in the longleaf ecosystem, Bill Gates couldn't afford to restore an intact ground cover. Only about 10% of the seed are commercially available. As I said, I've planted about 60 acres of wiregrass plugs and I've planted them about 3 ft in the drill, 12 ft rows…so I'm planting about 1,210 plugs per *acre and at about 20 cents a plug just for the wiregrass, that's an expensive hobby.*

–NGO interviewee

Most participants discussed a lack of funding concurrently with a lack of personnel – which combined hindered their agencies' ability to hire burn crews for implementing prescribed fire. Some participants also mentioned being unable to afford the financial and personnel resources to conduct gopher tortoise population or habitat surveys.

Conflicting intra-agency views

Conflicting intra-agency views was discussed as an operational restriction by over half of all participants (51.9%, n = 14, Table 3.3). Conflicting intra-agency views consisted of differing opinions within an organization on either how habitat should be managed, what techniques should be used to implement habitat management, or what land management objectives should be prioritized. More specifically, almost 60% of participants affiliated with federal, state, and NGOs (57.1%, n = 4 and 60%, n = 6; 57.1%, n = 4, respectively; Table 3.3) identified conflicting intra-agency views as a constraint to effective gopher tortoise habitat management. The following statement by a state interviewee demonstrates the internal tensions regarding habitat management:

We have internal challenges where structurally, our wildlife resources division has been focused on timber management in some areas, so we're shifting from that model to a more habitat-based approach… and there's been a steep learning curve for the staff who are more familiar with that older model. I'd say that our number one obstacle is to refocus, reeducate staff within the wildlife resources division who don't get or don't understand or don't like habitat restoration and as we are attempting to practice it.

Although a few participants acknowledged that sections or departments within an agency were slowly beginning to shift their management paradigm, many participants struggled to discuss this specific topic. Some participants were audibly frustrated while sharing their experiences of what they saw as mismanagement and failed efforts in expressing their concerns with higher management. One state participant shared the following experience:

> *[Forestry] can go into an area, and they've done it in the past, and completely nuke it for site preparation with really harmful chemicals where there's really good groundcover because their priority is making sure the tress that they're about to plant have no competition. That's happened multiple times and they've gotten their wrists slapped for doing it, but it happens often. And, many of the forest management plans, they have to have them reviewed by biologists, but it seems like they were always trying to get away with doing destructive things like root raking, bedding, and very heavy herbicide site preparation, stuff like that. I understand [what] their motivations are… they got hired to grow trees and make money for the state by cutting them down, so that's what they know to do, but there does seem to be some lack of recognition that the primary goal should be wildlife conservation. And forestry in many cases does improve habitat for wildlife, but it should only be done when it clearly is for the betterment of wildlife.*

No participants from private organizations, however, mentioned any conflicting intra-agency views. This seemed to be attributed to everyone within the hierarchy of the organization understanding that timber production was the overriding goal, and that any wildlife management was a secondary objective.

Time lag

During interviews, multiple participants noted that the sometimes-long transition period between property acquisition and the initiation of habitat management created a time lag during which no habitat management occurred. In recent years, organizations working in Georgia have made significant efforts to purchase large tracts of land for the purpose of conserving gopher tortoises; however, some natural resource professionals are beginning to raise concerns about managing the newly acquired properties in addition to properties they are already struggling to manage with limited financial and personnel support. It is important to note that participants also mentioned some of the new tracts purchased may have had little to no habitat management before purchasing; therefore, they could require more intensive (and expensive) management interventions than lands with longer histories under state, federal, or NGO ownership. Sixty percent of state participants and nearly 43% of NGO participants (60%, n = 6 and 42.9%, n = 3, respectively; Table 3.3) described experiencing this challenge:

> *…we're probably seeing a lag in the response of gopher tortoise population identification, then the property acquisition, and then after property is actually acquired you've got a lag time for the planning, the proposal, and then it might be a few years before you see anything touch the dirt. –State interviewee*

Landowner distrust and lack of information

Participants who interfaced with private landowners (*i.e.*, family forest owners, as opposed to large corporate or portfolio timberland owners) attributed landowner distrust in federal and state agencies and a lack of information on species or habitat needs as causes of inadequate gopher tortoise habitat management on private lands. A third of all participants

(33.3%, n = 9, Table 3.3) and over 70% of NGO participants specifically (71.4%, n = 5, Table 3.3), described these types of challenges with sentiments such as the following:

… folks who live in the United States have a fundamental distrust of [the] government. And, if you're a private landowner your distrust is probably heightened. And, if you distrust the government, there's probably a couple of levels. One of them is you distrust the state government more than your county government, but you really distrust the federal government more than the state. –Private interviewee

A theme emerged across interviews that many private landowners are wary of allowing federal, state or NGO agency representatives on their properties. This fear stems from the misconception that if gopher tortoises are found, a landowner will no longer have the right to manage their land – potentially interfering with their livelihood. Natural resource professionals attributed landowners' misconceptions and hesitancies to a lack of information about gopher tortoises and the resources available to help private landowners with habitat management. One participant stated:

When people talk to our biologist, they don't know why NRCS [Natural Resources Conservation Service] is restricting some of the practices because they have a gopher tortoise there, all they look at it "I have this tortoise and my practice is restricted." –NGO interviewee

Participants explained that once they are able to make a connection with a landowner, discuss the resources available and are allowed to help with the implementation of habitat management, landowners begin to open up to the opportunities of working with their organization – benefiting both gopher tortoise persistence on their land and the landowner's livelihood. Natural resource professionals cited that this relationship requires continuous nurturing and substantial coordination, but it ultimately plays a substantial role in gopher tortoise conservation.

Decision-making processes, planning and implementation of habitat management

Competing habitat management factors

When asked about competing factors that drive habitat management decisions, a pattern emerged across interviews, with the most frequently identified competing objectives being timber harvest, hunting, military mission, and other target species. All participants recognized the vital role gopher tortoises play as a keystone species. Throughout interviews, participants discussed how tortoise habitats are compatible with both common and imperiled flora and fauna. When asked how managing gopher tortoises ranks in terms of relative importance compared to other habitat or site management objectives, responses varied greatly. Responses were dependent on source of purchasing funds for property procurement, agency affiliation, and priorities of property ownership. In recent years, Georgia has made significant efforts to acquire properties to protect gopher tortoise populations and has made tortoise management a top priority on these properties. However, since gopher tortoises are not federally listed, habitat management on other properties was either focused on federally listed species (*e.g.,* RCWs, eastern indigo snakes) or the monetization of opportunities from hunting or timber harvest. Occasionally, the management of those properties, intended for purposes other than tortoise conservation, would align and benefit tortoise habitat needs.

Timber harvest

Timber harvest was the top competing factor driving habitat management (70.4%, n = 19, Table 3.4). Federal, state, and NGO participants discussed the importance of timber revenue for supplementing budgets. However, interviewed natural resource professionals were more concerned about harvesting timber in a way that benefits wildlife. In comparison, private participants (100%, n = 3, Table 3.4) shared sentiments such as the following:

> *Our primary objective is economic. … We're not trying to optimize gopher tortoise habitat, that's not our objective. Our objective is to maximize net present value. And, our objective is to maximize return for our shareholders and also be protective of gopher tortoise habitat and gopher tortoise populations. –Private interviewee*

Other target species

Other target species (*e.g.,* red-cockaded woodpeckers (RCWs), *Leuconotopicus borealis*; Bachman's sparrow, *Peucaea aestivalis*; eastern indigo snakes, *Drymarchon couperi*) were also mentioned by more than half of participants (59.3% n = 16, Table 3.3) as important management targets. Participants often made comments along these lines, regarding other threatened and endangered species:

> *It gives us a little more weight to say, "Hey, we've got to protect these guys [gopher tortoises] to manage these guys [indigo snakes]." Same with habitat. The more gopher tortoise habitat we can open up, the more potential indigo snake breeding area we've got. … So it's kind of a win-win for gopher tortoises when we're talking about managing for eastern indigo snake breeding and hunting habitat because it falls right in line with gopher tortoises, and vice-versa. –State interviewee*

Hunting

Many participants expressed similar beliefs that managing habitat for gopher tortoises was beneficial for some game species (*e.g.,* bobwhite quail, *Colinus virginianus;* wild turkey, *Meleagris gallopavo*; white-tailed deer, *Odocoileus virginianus*) and vice-versa; however, approximately 45% of those interviewed mentioned hunting and game species as a competing factor driving habitat management. Some participants also recognized the economic importance of hunting to the conservation efforts of tortoises.

> *Hunting is our division's largest source of income, but it's not just hunting, it's hunting and all the equipment associated with it, so our money is mostly excise taxes on guns, ammunition, scopes, hunting accessories. So that's where the majority of our operational budget comes from. That being said, game species management is our main driver on habitat projects, but gopher tortoises are definitely right there at the top because when we can pick an area that needs habitat modifications or enhancements that we know will benefit game species and will also benefit gopher tortoises, that ranks it higher than just a place that we could manage for game species. –State interviewee*

Military mission

Military mission was defined as military mission readiness, training, and land use for new construction of structures (*e.g.,* buildings, airfields, artillery ranges, etc.) to best support the military. Thirty-seven percent of all participants and nearly 72% of federal participants (37%, n = 10 and 71.4%, n = 5, respectively; Table 3.4) discussed military missions as a driving factor influencing habitat management. Gopher tortoise populations on military installations typically occur in buffer zones acquired by the military to prevent encroachment of development that could hinder training activities. The U.S. military branches have contributed substantially to gopher tortoise conservation efforts; however, several participants mentioned sentiments such as the following:

> *On a military installation, their primary mission is not land management, it's the military mission. So, when we burn these things, we create this really nice open habitat and it's in the upland [habitats where tortoises occur]...That poses a challenge because [when] they need to put in new buildings somewhere, that's the first place they're going to go look at. –Federal interviewee*

It is important to note that although tortoise habitat was said to often coincided with the best locations to install new structures, management of open and well-burned habitat is encouraged by military personnel because it supports military training operations, other target species (*e.g.,* RCWs and eastern indigo snakes), and gopher tortoises.

Performance measures and success of habitat management

Performance measures

Performance measures for gauging success of gopher tortoise habitat management included the following habitat metrics: pass / fail (an individual decides if habitat management is satisfactory or unsatisfactory), acres burned (number of acres set to burn each year), and thinning / harvest requirements (number of stands, acreage, or basal area requirements for thinning or harvest that are expected to be met). Metrics not based on habitat were performance measures based on the gopher tortoise populations themselves. Only one federal participant (3.7%, Table 3.5) mentioned that habitat management was assessed more on a pass or fail evaluation completed by the state's natural resource agency. Approximately, 19% of participants (18.5%, n = 5, Table 3.5) discussed meeting a set number or percentage of acres burned each year. Many participants aimed to burn 30-50% of burnable acres across property ownership types including military installations, state-owned properties and private family lands. A similar sentiment was shared by 11% of participants (n = 3) regarding thinning or harvest requirements where a set portion of stands were to be managed every year. On corporate private lands, this performance measure was only applied to properties that were specifically set aside for gopher tortoise conservation. This habitat metric, specific to tortoises, was not universally applied to properties that were managed primarily for economic objectives. Only one federal participant (3.7%, n = 1, Table 3.5) mentioned any performance measure based on gopher tortoise population metrics rather than habitat-based metrics. This participant revealed that on their military installation they conduct line-distance transect surveys every year on 20% of the installation where gopher tortoises occur – giving managers better insight into resident tortoise populations.

Timeline for management plans

The timeline for management plans set for gopher tortoise habitat varied from generalized 10-50 year management plans to more specific 1-5 year plans. A third of all participants (33.3%, n = 9, Table 3.5) discussed having long-term habitat management plans. A few state participants mentioned longer-term planning:

> *For the WMAs [Wildlife Management Areas] they're following the 50-year management plans, but some of those 50-year management plans were written 20 years ago and haven't been updated and have antiquated management suggestions or recommendations, requirements, guidelines. Others have been written more recently*

that have much better information and much more appropriate management information, so that's a mixed bag too. –State interviewee

However, since state agencies recognized this as a hindrance to effectively implementing habitat management, state agencies have recently embedded 10 year plans into the generalized 50 year plan as well. To further narrow down specific management objectives across properties, state agencies also establish annual work plans. One participant stated:

That's what the field staff does, they have better pull at the local level, all the variables that could potentially stand in their way of accomplishing, not permit, but slow the accomplishment of the goals. So, they have to adjust the timeline as they see fit in that 10 year plan to make them achievable. They [field staff] need to be objective in that 10 year plan and be specific that the [goals] are achievable. They know what they can achieve. –State interviewee

Federal agencies on military installations operate on 5 year Integrated Natural Resources Management Plans (INRMPs) and annual plans to build management direction on the military mission needs or environmental changes. Participants from NGOs only mentioned providing small private landowners with more generalized, long-term plans (42.9%, n = 3, Table 3.5) that are used as suggestions for landowners to manage for gopher tortoises. No corporate private landowner mentioned having short- or long-term management plans for gopher tortoises on properties where the primary objective was economic.

Accountability

Nearly 26% of participants (25.9%, n = 7, Table 3.5) described how their organization was held accountable for gopher tortoise management. Both state and federal agencies mentioned reviewing each other's management plans for input. Since state and federal organizations are participants in the Gopher Tortoise Candidate Conservation Agreement (CCA), they are also supposed to report annually whether they are meeting burning goals, habitat restoration or maintenance activities, and tortoise population assessments. One NGO (14.3%, n = 1, Table 3.5) stated that they have a science advisory committee to independently review their research to ensure the dispersal of information and implementation of best practices for gopher tortoise management. Corporate private landowners (66.7%, n = 2, Table 3.5) discussed two different methods for holding both their contractors and company accountable for habitat management. Contractors who are working on properties where gopher tortoises occur must undergo annual forest certification. This training consists of learning about threatened and endangered species and guidelines regarding how to properly maneuver heavy equipment without causing detrimental effects on tortoises or their burrows. The corporate private landowners interviewed were also all enrolled in a third-party sustainability certification scheme, the Sustainable Forest Initiative (SFI). Under SFI requirements, forest owners must verify that appropriate precautions were being taken to minimize the risk of harming tortoises. For example, landowners are required to mark GPS points of each burrow location on the property and flag trees that are near burrow entrances that if harvested or approached by heavy equipment could potentially collapse the burrow.

Discussion

There have been large initiatives to ensure gopher tortoise viability and representation across the species' range, including substantial land acquisition and population manipulations such as translocation and head-starting. More specifically in Georgia, The Gopher Tortoise

Conservation Initiative was established to restore and protect gopher tortoise habitat, thereby benefiting gopher tortoises, many other imperiled species and the longleaf pine ecosystem. However, the primary objective of this initiative it to prevent gopher tortoises from being listed on the ESA in parts of its range where it is currently a candidate species. To date, over $173 M has been raised by the state of Georgia, federal agencies, and private foundations to support this effort. Collaboratively, these organizations have permanently protected nearly 60 viable populations, out of a goal of 65, which includes the protection of 96,460 acres (Georgia Conservancy 2020). Throughout interviews, it became apparent that the habitat types natural resource professionals are currently managing were not representative of the ideal habitat conditions they described for gopher tortoises. Ideal tortoise habitat was briefly described as open canopy, xeric soils, and diverse herbaceous ground cover. However, the current conditions of many tortoise-occupied habitats were said to resemble densely planted pine plantations or mixed hardwood-pine with dense midstory and sparse herbaceous understory. Although land acquisition plays a large role in the conservation of gopher tortoises, habitat management remains key to continued persistence of tortoise populations across the state.

Prescribed fire, mechanical treatments (*e.g.*, stand thinning or harvest, roller chopping, etc.), planting (*e.g.*, trees, native ground cover, grasses), and chemical treatments (*e.g.*, use of herbicides) were identified as tools for managing gopher tortoise habitat; however, frequency and seasonality varied across and within organizations. The implementation of these techniques was also very dependent on a multitude of barriers and challenges faced by natural resources professionals. The top three operational restrictions identified in this study are limitations to applying prescribed fire, lack of capacity, and conflicting intra-agency views.

Limitations to applying prescribed fire was the most common challenge identified. Weather restrictions are increasingly becoming a hindrance to effective tortoise management due to smoke management issues and the potential for wildfire outbreaks near densely populated areas – which seems to be even more evident in tortoise-occupied sites near the coast and on military installations.

The challenge of applying prescribed fire is also linked to having insufficient personnel or funding (lack of capacity). In densely populated areas, some natural resource professionals expressed not having enough or any personnel (because some organizations must outsource burn crews) available to conduct prescribed burns within the narrow weather window conducive for burning, especially for growing season burns. Lack of capacity concerns were expressed across the majority of all organizations. Inter-agency burn teams and mobile "strike teams" have helped facilitate an increase of prescribed burning throughout Georgia; however, they are unable to keep up with the high demand. One solution to help mitigate this operational restriction across landowner types would be to call upon the assistance of local prescribed burn associations (PBAs) or university burn clubs – both of which typically have prior knowledge or certifications conducting burns, extra equipment, and resources to ease the burden on natural resource professionals. In addition, PBAs can significantly decrease the financial responsibility associated with prescribed burns (Diaz *et al.* 2016) and students from university burn clubs will oftentimes participate to gain experience.

Lastly, nearly 60% of federal, state and NGO interviewees reported conflicting intra-agency views as a constraint to effective habitat management for gopher tortoises. This seemed to be a result of differing educational backgrounds (*e.g.,* game vs. nongame vs.

forestry), work experiences and what habitat management objectives natural resource professionals were hired to achieve during their employment. Although most interviewees mentioned that habitat management plans for all properties, specifically tortoise-occupied sites, are typically approved by someone from each department within an organization, there still seems to be difference in how habitat is supposed to be managed and how it is actually being managed. Interviewee responses suggested that that disconnect potentially stems from multiple factors, including (1) the misinterpretation of agreed-upon management plans by those implementing management techniques, (2) differing ideas on what land management objectives should be prioritized, and (3) lack of intra-agency cross-training. Bringing all natural resource professionals – game and nongame biologists, botanists, foresters, land managers, alike – together and refocusing an organization's mission as a whole could prove beneficial to resolving some of these challenges. Additionally, providing natural resource professionals with cross-training or educational opportunities would allow for a more comprehensive understanding of differing departmental land management objectives. Regardless, it is imperative that those managing gopher tortoises either begin or continue to address operational restrictions, for they could ultimately affect the overall success of tortoise conservation in not only Georgia but the southeast.

Across interviews, how gopher tortoises ranked in terms of relative importance compared to other habitat or site management objectives varied. All interviewees recognized the importance of gopher tortoises as a keystone species. However, since gopher tortoises are not federally listed, habitat management on properties not purchased specifically for tortoise conservation either focused on federally listed species or on the monetization of opportunities from hunting or timber harvest. It is recognized that without supplemental funding from hunting or timber harvest conservation, efforts for gopher tortoises would not be as successful as they have been thus far, but this study suggests that these differing site management objectives could naturally coincide on properties where tortoises are not a top priority.

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Table 3.1 Number of natural resource professionals interviewed from management agencies working in Georgia, USA; including participant's years of experience with management of gopher tortoises (*Gopherus polyphemus*) and their respective habitats.

	Interviewees (*n*)
Management agency	
Federal	7
State	10
NGO	7
Private	3
Years of experience	
0 – 5	2
6 – 10	5
11 – 20	11
21 +	9

Table 3.2 Frequency of gopher tortoise (*Gopherus polyphemus*) habitat management techniques mentioned in interviews of natural resource professionals across agencies and organizations in Georgia, USA. Affiliations of interviewees include federal (n = 7), state (n = 10), non-governmental organizations (NGO, n = 7), and private (*e.g.*, electrical and timberland companies; n = 3). Management techniques include prescribed fire, mechanical (*e.g.*, stand thinning or harvest, roller chopping, etc.), planting (*e.g.*, trees, native ground cover, grasses), and chemical (*e.g.*, use of herbicides).

	Interviewees (*n*)				
	Federal	**State**	**NGO**	**Private**	**Percentage of Interviewees (%)**
Management techniques					
Prescribed fire	7	10	7	3	100.0 %
Mechanical	5	10	6	3	88.9 %
Planting	4	7	6	3	74.1 %
Chemical	3	6	5	3	63.0 %

Table 3.3 Summary of interviews (%) that were coded for specific barriers and challenges to decision-making and the implementation of habitat management for gopher tortoises (*Gopherus polyphemus*) in Georgia, USA. Affiliations of interview participants include federal (n = 7), state (n = 10), non-governmental organizations (NGO, n = 7), and private (*e.g.*, electrical and timberland companies; n = 3). Barriers and challenges include limitations to applying prescribed fire, lack of capacity, conflicting intra-agency views, time lag, and private landowner distrust and lack of information.

	Interviewees (*n*)				
	Federal	**State**	**NGO**	**Private**	**Percentage of Interviewees (%)**
Barriers & challenges					
Limitations to applying prescribed fire	5	8	2	3	66.7 %
Lack of capacity	2	8	5	1	59.3 %
Conflicting intra-agency views	4	6	4	0	51.9 %
Time lag	0	6	3	0	33.3 %
Private landowner distrust & lack of info.	0	3	5	1	33.3 %

Table 3.4 Competing factors driving habitat management other than gopher tortoise (*Gopherus polyphemus*) across and within agencies and organizations that manage for tortoises in Georgia, USA. Affiliations of interview participants include Federal (n=7), State (n=10), Non-governmental organizations (NGO, n=7), and Private (*e.g.*, electrical and timberland companies; n=3).

	Interviewees (*n*)				**Percentage of Interviewees (%)**
	Federal	**State**	**NGO**	**Private**	
Competing factors					
Timber harvest	3	7	6	3	70.4 %
Other target species	7	5	4	0	59.3 %
Hunting	2	6	2	2	44.4 %
Military mission	5	3	2	0	37.0 %

Table 3.5 Performance measures, timeline of management plans, and accountability of implementing gopher tortoise (*Gopherus polyphemus*) habitat management across and within agencies in Georgia, USA. Affiliations of interview participants include Federal (n=7), State (n=10), Non-governmental organizations (NGO, n=7), and Private (*e.g.*, electrical and timberland companies; n=3). Performance measures include Pass / fail, Acres burned, Thinning / harvest requirements, and Other. Performance goals include Generalized, 5 – 50 year plans; specific, 1 – 5 year plans; and both generalized and specific plans.

	Interviewees (*n*)				
	Federal	**State**	**NGO**	**Private**	**Percentage of Interviewees (%)**
Performance measures					
Pass / fail	1	0	0	0	3.7 %
Acres burned	3	2	0	0	18.5 %
Thinning / harvest requirements	2	0	0	1	11.1 %
Other	1	0	0	0	3.7 %
Timeline for management plans					
Generalized, 10-50 years	3	3	3	0	33.3 %
Specific, 1-5 years	2	3	0	0	18.5 %
Accountability	2	2	1	2	25.9 %

CHAPTER 4

CONCLUSIONS

Globally, turtle populations are rapidly declining due to a multitude of threats (Rhodin *et* al. 2018, Stanford *et al.* 2020). Because turtles are long-lived, slow to mature and have low offspring survival to adulthood they are especially vulnerable to anthropogenic perturbations and populations are slow to recover. Therefore, mitigation often requires multi-faceted conservation approaches (Crawford *et al.* 2020, Spencer *et al*. 2017). Population augmentation techniques may need to be implemented in addition to land management to recover or bolster populations in decline. Over the last century, gopher tortoise (*Gopherus polyphemus*) populations have experienced an estimated 80% decline (USFWS 2012) sparking many conservation initiatives throughout the southeast. Although translocation has been commonly used to augment gopher tortoise populations, head-starting is becoming increasingly popular and should be investigated further. Thus far, studies have primarily investigated only short term (≤ 1 year) head-starting (Tuberville *et al.* 2015, Tuberville *et al.* 2021, Quinn *et al.* 2018), with little attention to the potential survival benefits or any potential negative physiological consequences of head-starting for extended durations.

Chapter 2 evaluated a suite of physiological responses in gopher tortoises head-started for extended durations. Results show there were no systematic differences among concentrations of plasma and fecal corticosterone, heterophil:lymphocyte ratios and lactate between tortoises head-started for 2.5 and 3.5 years. Although head-starting tortoises for extended durations did not seem to present any negative physiological responses, measuring stress-associated hormones is still an important factor to consider in all conservation programs including translocation and reintroduction efforts (Teixeira *et al.* 2007). Fecal corticosterone was the best predictor of movement and fate of individual tortoises at the end of this study. Although effects on movement were small, this research suggests fecal corticosterone may help explain variation in post-release behavior and could serve as an important biomarker to further evaluate different methodologies and release protocols. However, before fecal corticosterone can become a widely accepted tool of evaluating physiological responses in gopher tortoises, the time frame a fecal corticosterone sample is representative of needs to be validated.

Chapter 3 evaluated different gopher tortoise management perceptions, potential restrictions or challenges land managers may encounter, as well as how and what role these factors play in tortoise management processes among and within natural resource management agencies across Georgia. There have been large initiatives to ensure gopher tortoise viability and representation across the species' range in Georgia, including substantial land acquisition and population manipulations such as translocation and head-starting. However, regardless of the effectiveness of reintroduction programs, habitat management plays a key role in the overall success of tortoise conservation. The pressure on Georgia's natural resource agencies to acquire land for their target of 65 viable tortoise populations to decrease chances of federally listing the gopher tortoise may be delaying the response time of active habitat management. This has potential to cause other cascading barriers to gopher tortoise management by diverting resources that are currently needed for effective habitat management. One solution to help mitigate limitations of prescribed burning and the lack of capacity across landowner types would be to support the development and use of local prescribed burn associations (Diaz *et al.* 2016) or university burn clubs. Providing cross-training or educational opportunities to both university students and natural resource professionals would allow for a more comprehensive understanding of different departmental or educational backgrounds (*e.g.,* game vs. nongame vs. forestry) – which could decrease or ease tensions and misunderstandings stemming from conflicting intra-agency views. Additionally, it is important to clarify the priority of gopher tortoise management within agencies with multiple missions. Habitat management specific to tortoises does not necessarily need to be implemented across the entirety of properties but should be implemented at least where tortoises are considered a priority.

Collectively, this research has identified some of the challenges and opportunities associated with head-starting and maintaining optimal habitat for gopher tortoises. Refining head-starting techniques and measuring physiological responses are important to the success of population augmentation; however, without on-going, active management of gopher tortoise habitat population augmentation will likely produce marginal results. In general, habitat management remains the cornerstone of any reintroduction effort and should warrant more attention when determining the success of gopher tortoise conservation.

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APPENDICES

Appendix A. All candidate models used to evaluate pre-release predictors (*e.g.*, plasma & fecal corticosterone, heterophil:lymphocyte ratios, lactate, duration in captivity) of post-release movement metrics in gopher tortoises (*Gopherus polyphemus*) head-started for 2.5 or 3.5 years (n = 23) that were released at Yuchi Wildlife Management Area, Burke County, Georgia, USA in April 2019. The model with the lowest AIC is the most parsimonious and is indicated by a ΔAIC = 0; however, all models with an ΔAIC < 2 were considered supported. Post-release movement metrics are indicated in bold, followed by the list of pre-release predictor variables. Statistically significant ($p \leq 0.05$) predictors are denoted by a *. The only pre-release predictors included in the top ranked models (highlighted in grey) are fecal corticosterone (Fecal cort) and duration in captivity (2.5 or 3.5 years); however, the other predictor variables included are plasma corticosterone (plasma cort), heterophil:lymphocyte ratios (HL ratios), and lactate. Post-release movement metrics consist of both continuous and discrete data. Continuous outcome variables include maximum distance moved (between tracking events), mean distance moved (per tracking event), and final displacement from release location (until the animal died, went missing, or until the onset of winter dormancy; 15 November). Discrete, count variables include days to establish first burrow (following release), surface activity (number of times a tortoise was found outside of a burrow divided by the total number of tracking events), burrow switching (number of unique burrows used by an individual divided by the number of tracking event that individual was found in a burrow). Values presented include model degrees of freedom (K), Akaike Information Criteria (AIC), delta AIC (ΔAIC), and Akaike weight (Weight), which displays the weight of each model in the candidate set.

Model	**K**	**AIC**	**ΔAIC**	**Weight**
Maximum distance moved (m)				
Fecal cort*	3	230.471	0	0.645
Duration in captivity + Fecal cort*	4	231.667	1.2	0.355
Null	2	276.880	46.4	0.000
Duration in captivity	3	277.558	47.1	0.000
HL ratios	3	278.680	48.2	0.000
Plasma cort	3	278.843	48.4	0.000

Lactate	3	278.879	48.4	0.000
Duration in captivity + Lactate	4	279.486	49.0	0.000
Duration in captivity + Plasma cort	4	279.556	49.1	0.000
Duration in captivity + HL ratios	4	279.557	49.1	0.000
Mean distance moved (m)				
Fecal cort	3	203.803	0	0.659
Duration in captivity + Fecal cort	4	205.118	1.3	0.341
Null	2	230.972	27.2	0.000
Duration in captivity	3	231.818	28.0	0.000
Plasma cort	3	232.398	28.6	0.000
Duration in captivity + Plasma cort	4	232.773	29.0	0.000
HL ratios	3	232.956	29.2	0.000
Lactate	3	232.962	29.2	0.000
Duration in captivity + HL ratios	4	233.403	29.6	0.000
Duration in captivity + Lactate	4	233.670	29.9	0.000
Final displacement from release location (m)				
Fecal cort*	3	252.565	0	0.724
Duration in captivity + Fecal cort*	4	254.492	1.9	0.276
Null	2	296.266	43.7	0.000
Plasma cort	3	296.947	44.4	0.000
Duration in captivity	3	297.747	45.2	0.000
Duration in captivity + Plasma cort	4	297.943	45.4	0.000
HL ratios	3	298.263	45.7	0.000
Lactate	3	298.225	45.7	0.000
Duration in captivity + HL ratios	4	299.674	47.1	0.000
Duration in captivity + Lactate	4	299.747	47.2	0.000
Days to establish first burrow				
Duration in captivity* + Fecal cort*	3	307.650	0	0.954

Fecal cort	2	313.692	6.0	0.046
Duration in captivity + Lactate	3	597.650	290.0	0.000
Lactate	2	608.562	300.9	0.000
Duration in captivity + Plasma cort	3	618.713	311.1	0.000
Plasma cort	2	622.196	314.5	0.000
Duration in captivity	2	636.221	328.6	0.000
Duration in captivity + HL ratios	3	637.819	330.2	0.000
HL ratios	2	639.247	331.6	0.000
Null	1	641.172	333.5	0.000
Surface activity				
Duration in captivity* + Fecal cort*	3	139.0883	0	1.000
Fecal cort	2	161.0685	21.98	0.000
Duration in captivity + Lactate	3	192.3349	53.25	0.000
Lactate	2	201.9018	62.81	0.000
Duration in captivity	2	205.1255	66.04	0.000
Duration in captivity + HL ratios	3	205.6572	66.57	0.000
Duration in captivity + Plasma cort	3	206.4352	67.35	0.000
HL ratios	2	224.8188	85.73	0.000
Null	1	225.0291	85.94	0.000
Plasma cort	2	225.9943	86.91	0.000
Burrow Switching				
Duration in captivity + Fecal cort	3	104.202	0	0.595
Fecal cort	2	105.003	0.8	0.399
Lactate	2	115.127	10.9	0.003
Duration in captivity + Lactate	3	116.774	12.6	0.001
HL ratios	2	117.469	13.3	0.001
Duration in captivity + HL ratios	3	118.331	14.1	0.001
Null	1	118.627	14.4	0.000
Plasma cort	2	120.211	16.0	0.000

Duration in captivity	2	120.626	16.4	0.000
Duration in captivity + Plasma cort	3	122.205	18.0	0.000

Appendix B. Fate models to evaluate which predictors (duration in captivity, MCL, post-release movement metrics) have the greatest effect on post-release fate (1 = alive, 0 = dead) of gopher tortoises (*Gopherus polyphemus*) head-started for 2.5 or 3.5 years that were released at Yuchi Wildlife Management Area, Burke County, Georgia, USA in April 2019. The model with the lowest AIC is the most parsimonious and is indicated by a ΔAIC = 0; however, all models with a ΔAIC < 2 were considered supported. The top ranked models are highlighted in grey and statistically significant ($p \leq 0.05$) predictors within those models are denoted by a *. Model terms include MCL (midline carapace length in mm at release), Duration in captivity (2.5 or 3.5 years), Max dist moved (maximum distance moved between tracking events), Mean dist moved (mean distance moved per tracking event), Final displacement (final distance from release location until the animal died, went missing, or until the onset of winter dormancy, or 15 November), Days estab B (days to establish first burrow following release, and SA (surface activity, or the proportion of tracking evens that an individual was on the surface). Values presented include model degrees of freedom (K), Akaike Information Criteria (AIC), delta AIC (ΔAIC), and Akaike weight (Weight), which displays the weight of each model in the candidate set.

Model	K	AIC	ΔAIC	Weight
Fate				
MCL + Final displacement*	2	22.330	0	0.214
Duration in captivity x Mean dist moved	4	23.387	1.058	0.126
MCL x Final displacement	3	24.211	1.882	0.084
MCL + Mean dist moved	2	24.226	1.896	0.083
Duration in captivity + Final displacement	3	24.785	2.455	0.063
Final displacement	1	24.901	2.571	0.059
MCL x Days estab B	3	25.346	3.017	0.047
MCL x Mean dist moved	3	25.942	3.612	0.035
Days estab B	1	26.043	3.713	0.033
MCL + Max dist moved	2	26.177	3.847	0.031
Mean dist moved	1	26.368	4.039	0.028
Duration in captivity x Final displacement	4	26.509	4.179	0.027
Maximum dist moved	1	27.002	4.672	0.021
Duration in captivity + Mean dist moved	3	27.087	4.757	0.020
MCL + Days estab B	2	27.244	4.914	0.018

SA	1	27.250	4.920	0.018
MCL + SA	2	27.397	5.067	0.017
MCL x Max dist moved	3	27.900	5.571	0.013
Duration in captivity + Days estab B	3	28.699	6.370	0.009
Duration in captivity x Days estab B	4	28.916	6.586	0.008
Duration in captivity + SA	3	28.925	6.595	0.008
Duration in captivity + Max dist moved	3	28.962	6.632	0.008
MCL x SA	3	29.392	7.062	0.006
Null	1	29.526	7.196	0.006
Duration in captivity x Max dist moved	4	29.674	7.344	0.005
MCL	1	29.691	7.361	0.005
Duration in captivity x SA	4	30.836	8.507	0.003
Duration in captivity	2	31.391	9.061	0.002

Appendix C. University of Georgia's Human Subjects Office Institutional Review Board (IRB) approved interview questionnaire (PROJECT00001820). This semi-structured questionnaire was used to complete the interview process and to elicit perceptions of land management needs for ideal gopher tortoise habitat and potential operational restrictions to implementing land management actions. **Questions in bold text are mandatory, all others are optional.**

1. **Introduction**
    - **1.1. Background information: What is your current position and background? (prompts: agency, job description, # of years in position, previous experience, education)**
    - **1.2. How does your current position/work relate to gopher tortoises and managing gopher tortoise habitat?**
    - **1.3. Does [name of management property] currently have any strategies or policies geared specifically towards the conservation of gopher tortoises and management of their respective habitat?**

2. **Topic: Habitat management perceptions**
    - **2.1. Where do you obtain information about habitat needs of gopher tortoises (e.g., literature, personal observation/experience, species expert, etc.)?**
    - **2.2. What do you consider compatible or ideal gopher tortoise habitat to be?**
    - **2.3. Currently, what are the habitat types that you manage for gopher tortoises?**
    - **2.4. What habitat structure/habitat metrics are you trying to achieve?**
        - **2.4.1. What mechanisms do you use to manage tortoise habitat (e.g., prescribed fire, mechanical or chemical thinning, planting native grasses, etc.)?**
        - 2.4.2. How frequent are these tools being implemented?
            - 2.4.2.1. What time of year do you typically prescribed fire?
        - 2.4.3. In your experience, what mechanism(s) and the frequency in which it is implemented worked best for obtaining or maintaining tortoise habitat?
    - **2.5. Have you experienced barriers or challenges in effective habitat management for gopher tortoises?**

3. **Topic: Decision-making, planning, and the implementation of habitat management**
    3.1. **Where does funding come from for tortoise management?**
        3.1.1. **[For private owners:] Is your land enrolled in any formal conservation agreement or program? Does this provide any incentives or resources for gopher tortoise management?**
    3.2. **What are other factors that drive your habitat management decisions (e.g., hunting, military training, timber harvest, other target species, etc.)?**
    3.3. **How does managing for gopher tortoises rank in terms of relative importance compared to other habitat or site management objectives?**
    3.4. **At what scale are these decisions made? Do you / does this office have the authority to decide how the land is managed or are those decisions made at other levels or through other processes?**
    3.5. **How many properties do you manage? Are the opportunities and constraints the same or different across those properties?**
    3.6. **What other people or positions do you interface with within your own organization when making decisions about or implementing habitat management?**
        3.6.1. **How do they aid in making or implementing management decisions?**
        3.6.2. Do you receive specific management instructions or are you able to make executive decisions on what, when, and how management should occur?
    3.7. **Do you collaborate or interact with other agencies or people outside your organization when making land management decisions and/or implementing habitat management?**
        3.7.1. **How do they aid in making or implementing management decisions?**
    3.8. **Are there additional people within or outside of your organization you think you should be interfacing with?**
        3.8.1. How would these connections / collaborations benefit effective management?

4. **Topic: Performance measures of habitat management success**
    - **4.1. Are there specific goals set each year to obtain or maintain ideal gopher tortoise habitat needs or do you follow a generalized long-term management plan?**
        - 4.1.1. Who determines specific goals?
        - 4.1.2. When was the long-term management plan created?
    - **4.2. How often are resident tortoise populations and their respective habitats assessed?**
        - **4.2.1. Are there particular indicators that you use to measure success in achieving ideal tortoise habitat?**

5. **Topic: Looking forward**
    - **5.1. What role does your organization / property / agency play in the initiative to prevent an Endangered Species Act listing through proactive tortoise conservation? How well do you think you / your organization has met your obligations or commitments to this effort?**
        - **5.1.1. Do you think there is anything further that should be done to aide in conservation efforts of gopher tortoises?**
    - 5.2. Who else should we speak to about these topics?

Appendix D. Codebook used as a guide to facilitate qualitative data analyses of transcribed interviews (n = 27) using Dedoose software (Dedoose, Manhattan Beach, California, USA). Coded transcripts were used to identify emergent patterns across and within agencies or organizations. As data collection progressed, interpretations of qualitative patterns were further refined. Codes (n = 61) are representative of themes around perceptions of gopher tortoise habitat, how that habitat should be managed, best working practices for and within each agency's or organization's land management objectives, and operational restrictions to implementing effective management.

Objective 1: Describe & compare habitat management perceptions across & within state & federal agencies, timberland companies, & NGOs.

- **Obtain habitat info** – where practitioners obtain GT habitat info
- **Compatible/ideal habitat** – views on what kind of habitat(s) are compatible or ideal for GTs
- **Management techniques** – different techniques used to implement habitat management
  - **Prescribed fire**
  - **Mechanical** – thinning, roller chopping, "site prep," etc.
  - **Chemical** – herbicide use
  - **Planting** – trees, grasses
- **Awareness** – outreach, info. packets, social media, site visits, etc.
- **Mitigation bank** – set aside property that is specially designated for GT conservation/research
- **Operational restrictions** – barriers & challenges of decision-making & the implementation of habitat management for gopher tortoises
  - **Lack of funding** – inadequacy or inability to effectively and/or efficiently execute habitat management needs
  - **Lack of personnel** – inadequacy or inability to effectively and/or efficiently execute habitat management needs
  - **Conflicting intra-agency views** – differing opinions within an agency or organization on either how habitat should be managed, what techniques should

be used to implement habitat management, and/or what land management objectives should be prioritized

  - **Limitations to applying prescribed fire** – temporal or spatial factors inhibiting the ability to burn so concerns of weather, smoke management, or the inability to acquire sufficient liability insurance
  - **Time lag** – the lack of management due to the influx of property acquisitions in relation to the lack of resource availability
  - **Private landowner distrust & lack of information** – management difficult to achieve on private lands because landowners distrust involvement of government/agency or lack information on proper species or habitat management needs
- **Expensive land acquisition** – land for GT conservation is getting more difficult to acquire due to an increase in development driving up real estate prices
- **State political reform** – management difficult to achieve/afford due to difficulties with state legislation

Objective 2: Evaluate decision-making processes, planning & the implementation of habitat management.

- **Policy** – any policy related to GTs & GT habitat management
- **Funding**
  - **Source**
  - **Incentives – Yes** – agency/organization that receives financial incentives for GT management
  - **Incentives – No** – agency/organization that does not receive financial incentives for GT management
- **Other driving factors** – competing factors driving habitat management other than GTs
  - **Military mission** – military mission readiness, training, land use for new construction of buildings, etc.
  - **Hunting** –habitat management for hunters and game species
  - **Timber harvest** – land use for timber revenue

- **Other target species** – habitat management focused on other target species (*i.e.*, RCWs, eastern indigo snakes, etc.)

- **GT relative importance rank** – how GTs rank in terms of relative importance in comparison to other habitat management objects
- **Decision-making** – scale at which decisions are made about GT habitat management
  - **Different entity** – habitat management decisions made by a different agency/organization/section than interviewee
  - **Group effort** – habitat management decisions made thru group efforts of interviewee's agency & other agencies/organizations/sections
  - **Higher management** – habitat management decisions made by higher management within interviewee's agency
  - **Lower management** – habitat management decisions made by lower management within interviewee's agency
  - **Self w/ discretion** – habitat management decisions made by individual w/ discretion
- **Implementation** – individual(s) implementing GT habitat management
  - **Different entity outside organization** – implementation of habitat management by a different entity outside of interviewee's agency/organization
  - **Different entity w/in organization** – implementation of habitat management by a different entity within an interviewee's agency/organization
  - **Group effort w/ outside organization** – implementation of habitat management by both entities outside of & within interviewee's agency/organization
  - **Group effort w/in organization** – implementation of habitat management by multiple entities within interviewee's agency/organization
  - **Self w/ discretion** – implementation of habitat management by self w/ discretion
- **Collaboration** – agencies/organizations/sections working together to implement GT habitat management

    - **Across & w/in** – collaboration efforts on GT management outside & within interviewee's agency
    - **Across boundaries** – collaboration efforts on GT management outside of interviewee's agency
    - **W/in organization** – collaboration efforts on GT management within interviewee's agency

Objective 3: Determine performance measures & success of habitat management.

- **Expectation metric** – performance measures set for habitat management
    - **Acres burned** – specific # of acres set to be burned each year
    - **Thinning / harvest requirements** – specific # of stands, acreage, or basal area requirements for thinning or harvest that are expected to be met
    - **Pass / fail** – an individual decides if habitat management is satisfactory or unsatisfactory
    - **Other** – any performance measure different than the above (ie., conducting line-distance transect surveys on a percentage of GT habitat per year)
- **Goals** – management plans or goals set for GT habitat
    - **Both** – specific & generalized management plans/goals for GT habitat
    - **Specific, yearly** – 1-5 year management plans
    - **Generalized, long-term** – 10-50 year management plans
- **GT habitat & pop assessed** – how often GT habitats and populations are assessed
- **Accountability** – how agency/organizations are held accountable for GT management

Objective 4: Assess different roles state & federal agencies, timberland companies, & NGO's play in the future of gopher tortoise conservation.

- **Initiatives to prevent listing** – what initiatives are the agency/organization taking to prevent the federal listing of GTs throughout the remainder of the range
- **Incentives to prevent listing** – what are the agency's/organization's incentives for preventing the listing of the GT

- **Commitments met?** – how well interviewee thinks agency has met obligations or commitments to the initiative of conserving GTs
- **Further efforts** – further efforts that should be done to aide in the conservation of GT & their respective habitats