FROM SNAKES TO SCAVENGERS: EFFECTS OF THE FUKUSHIMA DAIICHI NUCLEAR ACCIDENT

by

HANNAH CARISE GERKE

(Under the Direction of James C. Beasley)

Despite being one of the largest anthropogenic releases of radionuclide contamination in history, the ecological ramifications of the 2011 nuclear accident in Fukushima, Japan remain largely unknown. To understand how the evacuation and shift in human activity has affected wildlife communities, I characterized the vertebrate scavenging community in the FEZ and surrounding unaffected areas and tested the effects of carcass size, habitat, and human activity on the composition and efficiency of vertebrate scavengers. Despite the radiological contamination, the FEZ supports a diverse and efficient scavenger community. I then focused on scavengers for which limited data exist – snakes – and investigated their spatial ecology and factors influencing radiocesium accumulation and dose. My results demonstrate snakes accumulate highly variable radiocesium concentrations depending on local environmental contamination levels. Variation in habitat use and movement behavior substantially influences dose estimates, but accounting for environmental contamination within the home range can reduce uncertainty in dose estimations.

INDEX WORDS: Anthropogenic, Carrion, Habitat Selection, Home Range, Mesocarnivore, Radiation, Radiocesium, Scavengers, Spatial Ecology

FROM SNAKES TO SCAVENGERS: ANTHROPOGENIC IMPACTS TO WILDLIFE IN FUKUSHIMA, JAPAN

by

HANNAH CARISE GERKE

B.S., Texas A&M University, 2017

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2019

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by

HANNAH CARISE GERKE

Major Professor:	James C. Beasley
Committee:	J. Whitfield Gibbons
	John C. Maerz

Electronic Version Approved:

Ron Walcott
Interim Dean of the Graduate School
The University of Georgia
December 2019

ACKNOWLEDGEMENTS

This thesis would not have been possible without all the people who contributed their support. First and foremost, I would like to thank my advisor, Jim Beasley, for offering me the opportunity to grow and learn in the form of an international research project in a country I had always dreamed of visiting. Without the guidance of Jim, Tom Hinton, and my committee members John Maerz and Whit Gibbons, this research would not have been successful. I would like to thank everyone at the Savannah River Ecology Laboratory and my colleagues at the Institute of Environmental Radioactivity for their assistance (thank you, Hiroko-san!). I would also like to acknowledge the scholarships and funding provided by the Warnell School of Forestry and Natural Resources at the University of Georgia and the U.S. Department of Energy. A special thanks to Wes Dixon for all the blood, sweat, and tears shed in the Fukushima Exclusion Zone to get the data for my thesis. This project would have been a lot more difficult without your unfailing morale and reminders to laugh and take joy in the little things. Finally, I would like to thank the rest of my friends and family, who supported me every step along the way. I am particularly grateful to Troy Koser and Putter Tiatragul, whose willingness to lend an ear has been instrumental in keeping me sane these past two and half years, and to the endless encouragement and faith of my parents that helped me persevere. In the words of my grandfather, Garrett W. Maxwell: “Onwards and Upwards!”

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Over the last several decades, anthropogenic activities have caused rapid biodiversity losses that increase the likelihood of irreversible changes to ecosystem services and stability (Elmqvist et al. 2003, Ceballos et al. 2015). With the majority of the earth's surface directly impacted by humans (Sanderson et al. 2002), it is essential that we understand factors affecting the stability of ecosystems and their ability to provide biologically and socioeconomically valuable ecosystem services. The ways in which humans modify ecosystems and alter biodiversity are varied, ranging from direct impacts like habitat destruction and pollution to indirect effects like changes in population growth or migration (Millennium Ecosystem Assessment 2003).

The Fukushima Exclusion Zone (FEZ) offers a unique opportunity to study how ecosystem processes are impacted by contaminants and massive shifts in anthropogenic activity. In 2011, a 9.0-magnitude earthquake struck off the northeastern coast of Japan, damaging the Fukushima Daiichi Nuclear Power Plant and resulting in one of the most significant releases of anthropogenic radiological contamination in history (Steinhauser et al. 2014). The subsequent evacuation consisted of almost 120,000 people fleeing the area surrounding the power plant, and although radiation has decreased to safe levels to allow repopulation in some portions of the region, evacuation orders still remain for the FEZ where contaminant levels are too high for human habitation (Ohnishi 2011). Today, the FEZ stretches over approximately 371 km^2 of land

(Fukushima Prefectural Government 2019) and has substantially less human activity compared to the surrounding landscape.

The Fukushima Daiichi nuclear accident has been a catalyst for radioecological research regarding the impacts of radionuclide releases into the environment, but few researchers have evaluated how the anthropogenic aspects of the accident (e.g., evacuation of humans) have affected ecosystem processes. Recent work suggests that despite the presence of nuclear contamination, wildlife populations in the FEZ are not significantly different from those outside the FEZ (Lyons et al. In Press). In fact, some species are even flourishing, suggesting the lack of human activity can outweigh the effects of chronic low-dose radiation. In particular, wild boar (*Sus scrofa*) and other species routinely in conflict with humans are more abundant inside the FEZ than in the surrounding landscape (Lyons et al. In Press). Thus, while the 2011 nuclear accident and subsequent evacuation represent a large disturbance that has potentially altered ecological processes, evidence of rewilding in affected areas may be an indication of ecosystem resilience. Similar observations of thriving wildlife populations, including species that are rare and/or heavily persecuted by humans in other areas, have been reported in the Chernobyl Exclusion Zone (IAEA 2006, Deryabina et al. 2015, Webster et al. 2016, Schlichting et al. 2019) and the Korean Demilitarized Zone (Kim 1997, Kim and Cho 2005). Wildlife species that come into conflict with humans are often those that are also influential in the ecosystem.

Vertebrate scavengers are a component of biodiversity that support ecosystem function by providing services such as nutrient cycling and carcass removal, but are often vulnerable to human activity (Beasley et al. 2015). Scavengers serve as an essential stabilizing force in most ecosystems by increasing the complexity of food webs (Millennium Ecosystem Assessment 2003, Wilson and Wolkovich 2011). The functional role of scavengers in ecosystems has traditionally been underestimated, but many taxonomic groups (e.g., birds, rodents, carnivores, reptiles, arthropods, etc.) exhibit scavenging behavior (DeVault et al. 2003). Facultative scavenging is a common strategy in part because carrion is a high-quality resource that requires less energy expenditure than predation (Wilson and Wolkovich 2011). The presence of multiple species that function in similar ways within the scavenging community causes the ecosystem to be functionally redundant and supports food web persistence during stochastic events (Mori et al. 2013, Huijbers et al. 2015). For example, consumption of carrion by vertebrate scavengers retains nutrient standing stocks in higher trophic levels rather than allowing those stocks to return to the detrital pool, and the availability of carrion resources may supplement many species' diet and sustain populations during periods of limited food resources (Wilmers et al. 2003, Wilmers and Post 2006). Carrion may also increase population growth rates of scavengers, which in turn enhances their ability to exert top-down pressure on prey populations and stabilize food webs (Wilson and Wolkovich 2011).

Unfortunately, the vulnerability of vertebrate scavengers to anthropogenic activities means that alterations to scavenging guilds can cause cascading impacts on the environment (Beasley et al. 2015, O'Bryan et al. 2019, Sebastian-Gonzalez et al. 2019). The recent collapse of vulture populations in India following mass accidental poisoning presents a sobering example of the functional role of scavengers, where vulture declines lead to an increase in carrion resources that majorly expanded feral dog (*Canis familiaris*) and rat (*Rattus rattus*) populations. The eventual result was a human health crisis from increased rabies exposure (Ogada et al. 2012). Several studies have shown significant impacts of anthropogenic activities on scavenging dynamics, including altered efficiency (carcass removal) (DeVault et al. 2011, Olson et al. 2012, Huijbers et al. 2013), activity patterns (Huijbers et al. 2015), and shifts in scavenger composition

(Tan and Corlett 2012, Huijbers et al. 2015, Sebastian-Gonzalez et al. 2019), occupancy (Twining et al. 2017), or dominance (DeVault et al. 2011). Thus, understanding how anthropogenic disturbances influence vertebrate scavengers and their role in the ecosystem remains a priority (Barton et al. 2013, Beasley et al. 2015). Studying scavenging dynamics in the FEZ will further our understanding of wildlife communities and nutrient flow in a contaminated system as well as provide implications for ecosystem health and stability.

Although numerous anecdotal records exist in the literature (Capula et al. 1997, Shivik and Clark 1999, Lillywhite et al. 2008, Ayres 2012, Golla and Durso 2015), scavenging by snakes was traditionally believed to be an uncommon behavior (DeVault and Krochmal 2002). However, scavenging appears to be an intentional foraging strategy in several snake species and recent work asserts that scavenging is more prevalent in many species than previously assumed (Shivik and Clark 1997, DeVault and Krochmal 2002). It is also possible some snakes may have evolved detoxification strategies to overcome toxins produced by microbial competitors in order to utilize carrion (Krochmal 2005, Shivik 2006). Due to their slow metabolism, ability to persist long periods of time on few meals, and reliance on chemosensory cues, snakes may be well-suited to taking advantage of carrion resources (Shivik and Clark 1997, DeVault and Krochmal 2002). One study examining the effects of a carcass's spatial position found snakes to be the dominant vertebrate scavenger of nestling birds (Smith et al. 2017), indicating snakes can play a vital role as scavengers in some ecosystems.

As scavengers and strict carnivores, snakes exhibit several traits that make them vulnerable to contaminants, including small home ranges, site fidelity, longevity, and high trophic status (Hopkins 2000, Campbell and Campbell 2001;2002). Despite the surge of interest in determining the effects of chronic low-dose radiation to wildlife following the 2011 nuclear accident in Fukushima (Hinton et al. 2013, Bréchignac et al. 2016, Stark et al. 2017, Beresford et al. 2019), there is a startling lack of research regarding the effects of contaminants on snakes (Hopkins 2000, Campbell and Campbell 2001;2002). Basic information necessary for evaluating effects of radiation – such as radioactive nuclide (radionuclide) activity concentrations, radionuclide transfer, and dose estimates – remain scarce or missing (Wood et al. 2010, Wood et al. 2012). The physiological processes of poikilothermic reptiles are distinct from those of other taxa, causing differences in metabolism, contaminant uptake/accumulation, and biological half-life that may necessitate different toxicity thresholds for some contaminants and influence whole-body activity concentrations (Staton et al. 1974, Campbell and Campbell 2002, Beresford and Wood 2014). For radiocesium – one of the most common, long-lasting radionuclides remaining in many radiologically contaminated areas – only a handful of reports on activity concentrations or dose rates are available for snakes. Most of these data have been collected from the Savannah River Site in the US (Brisbin et al. 1974, Staton et al. 1974, Bagshaw and Brisbin Jr 1985, Brown et al. 2016b), with a few specimens from Chernobyl (Barnett et al. 2009, Oskolkov et al. 2011) and one from Fukushima (Fuma et al. 2017). Brisbin et al. (1974) found snakes to have the highest radiocesium concentration of any naturally occurring vertebrate predator reported at the time, suggesting snakes could accumulate high levels of radiocesium. Given the scarcity of data on radiological contaminants in snakes, the factors influencing radiocesium accumulation and radiation dose in snakes are not clear.

Dose assessments require detailed knowledge of an individual's radiation exposure, yet despite advances in technology, large uncertainties remain in our ability to accurately estimate radiation doses for many species (Stark et al. 2017, Anderson et al. 2019, Hinton et al. 2019). One complicating aspect of dose estimations is that the total radiation dose an organism is exposed to is comprised of a combination of internal and external dose, each of which is influenced by a myriad of factors. Internal dose rates occur through ingestion of radionuclides that either pass through the gastrointestinal track or are incorporated into the organism's tissues. Uncertainties associated with internal dose rates are increased by variation in age, diet, uptake and accumulation rates, and the state of equilibrium between radionuclides in the organism and its surroundings (Forseth et al. 1998, Malek et al. 2004, Ishii et al. 2017, Stark et al. 2017, Nemoto et al. 2018). An organism's external dose is primarily influenced by its exposure to radionuclides in the environment, which are heterogeneously distributed across the landscape (Koarashi et al. 2016, Imamura et al. 2017, Kato et al. 2018). Potential exposure to contaminants can vary substantially among individuals and species across the landscape due to differences in movement behavior and habitat use (Hinton et al. 2015, Imamura et al. 2017, Aramrun et al. 2019), but despite this variability, factors like species-specific movement behavior and space use are often unaccounted for in risk assessments or estimation of external dose rates (Gaines et al. 2005, Stark et al. 2017).

For some species, movement behavior cannot be incorporated into dose assessments because their spatial ecology is not well-studied. This is the case for Japanese rat snakes (*Elaphe climacophora* and *E. quadrivirgata*), which are abundant within the FEZ. Some snake species exhibit selection for particular vegetation types or landscape features like forest edges for thermoregulation and foraging (Blouin-Demers and Weatherhead 2001, Row and Blouin-Demers 2006, Lelièvre et al. 2010). If rat snakes in the FEZ select portions of the landscape that correspond to higher environmental contaminant levels, this may increase their radiation exposure as well as the probability of ingesting prey with higher radiocesium concentrations.

Knowledge of movement and habitat selection within contaminated areas like Fukushima is critical for estimating dose estimates and patterns of radionuclide accumulation in snakes.

Dose estimates are often calculated using computer simulation software (e.g., ERICA; Environment Risk from Ionising Contaminants Assessment and Management) that incorporate data available on radionuclide activity concentrations in the organism and/or the environment (Brown et al. 2008, Brown et al. 2016a), but these estimates are often associated with large uncertainties due to the natural variabilities discussed above as well as reliance on default parameters generated from limited data sources. A growing number of studies are trying to account for uncertainties in wildlife dose estimations by comparing estimated doses to absorbed dose from dosimeters placed in the environment (Stark and Pettersson 2008, Fuma et al. 2015, Kubota et al. 2015) or on animals (Chesser et al. 2000, Beresford et al. 2008, Hinton et al. 2015, Aramrun et al. 2019, Hinton et al. 2019), but this has not yet been attempted for snakes.

The goal of my thesis research was to broaden our understanding of repercussions from the 2011 Fukushima Daiichi Power Plant accident by investigating both the impacts of shifts in human activity on scavenger communities as well as the radiological contaminant burdens and dose estimates of a common scavenger, snakes. In the present chapter, I presented a literature review that explains the connections between scavengers and snakes, as well as the critical need for research investigating snake habitat use as it relates to radionuclide accumulation and dose estimations. In Chapter 2, I characterize the vertebrate scavenger community in Fukushima and test the effects of carcass size, habitat, and human activity on scavenging dynamics. By examining wildlife community composition and scavenger efficiency, my research has the potential to greatly advance our knowledge of how anthropogenic activities influence food web dynamics, informing the extent to which human presence results in cascading effects on ecosystem services like carcass removal and nutrient cycling. In Chapter 3, I describe the movement behavior, home range sizes, and habitat selection of rat snakes tracked with GPS-transmitters in the contaminated FEZ, which is an essential first step to understanding their radiation exposure. Finally, in Chapter 4 I discuss factors influencing radiocesium activity concentrations and dose estimations of snakes. My research represents one of the most comprehensive radioecological studies of snakes to date, and has implications for reducing uncertainty in assessments of dose and risk to reptiles in radiologically contaminated areas. This research addresses one of the greatest challenges in radioecology by quantifying external exposure of wildlife in relation to their spatiotemporal habitat use (Hinton et al. 2015).

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CHAPTER 2

EFFECTS OF ANTHROPOGENIC ACTIVITY ON THE EFFICIENCY AND COMPOSITION OF VERTEBRATE SCAVENGING COMMUNITIES IN FUKUSHIMA, JAPAN

Gerke, H.C., T.G. Hinton, K. Okuda, and J.C. Beasley. To be submitted to Anthropocene.

ABSTRACT

The 2011 Nuclear Disaster in Fukushima, Japan resulted in one of the most significant anthropogenic releases of radiological contamination in history, triggering the evacuation of almost 120,000 people. Much of the Fukushima Exclusion Zone (FEZ) remains devoid of human habitation, provoking the question – how has the presence of radiological contamination and change in human activity impacted wildlife communities and ecosystem functions? The objective of this study was to characterize the vertebrate scavenging community in the FEZ compared to surrounding unaffected areas, and elucidate the effects of carcass size, habitat, and human activity on the composition and efficiency of vertebrate scavengers. During summer 2018, we deployed remote cameras at carcasses placed in the FEZ and a nearby reference area. We conducted a total of 300 trials (200 mouse and 100 rabbit carcasses) balanced across two habitats (deciduous hardwood, evergreen conifer forest) in each zone, and quantified carcass fate, vertebrate scavenger species, time to first scavenging event, and time until carcass depletion. We recorded 13 vertebrate scavenger species (mostly mammals) with field mice (*Apodemus speciosus*), raccoon dog (*Nyctereutes procyonoides*), wild boar (*Sus scrofa*), and masked palm civet (*Paguma lavarta*) composing the most frequent scavengers observed. Species richness and carcass removal rates (72%) were similar between the evacuated FEZ and our inhabited reference area. We observed slight differences in scavenging rates of some species like boar and fox, which may have implications for nutrient distribution. Carcass size was a more important predictor of species richness, scavenger community composition, detection time, and persistence time than habitat or zone, although rabbit carcasses were detected faster outside the FEZ. Rain also significantly increased the persistence time of both carcass sizes. Our results suggest that despite the radiological contamination, the FEZ supports a highly diverse and

efficient community of scavengers, lending support to previous studies examining wildlife populations in radiologically contaminated areas with limited human activity.

INTRODUCTION

Over the last several decades, anthropogenic activities have caused rapid biodiversity losses (the ‘sixth mass extinction’), increasing the likelihood of irreversible changes that impair ecosystem services and stability (Elmqvist et al. 2003, Ceballos et al. 2015). With 83% of the world’s land directly impacted by humans (Sanderson et al. 2002), recognizing factors affecting the stability of ecosystems and their ability to provide biologically and socioeconomically valuable ecosystem services is essential. Vertebrate scavengers are a component of biodiversity that offer ecosystem services such as nutrient cycling and carcass removal, but many scavengers are vulnerable to anthropogenic activities (Beasley et al. 2015). In most ecosystems, scavengers are an essential stabilizing force because they increase the complexity and reticulate nature of food webs by providing large numbers of interspecies links (Millennium Ecosystem Assessment 2003, Wilson and Wolkovich 2011). A high degree of overlap within the scavenging community results in increased functional redundancy that can support food web persistence during stochastic events (Mori et al. 2013, Huijbers et al. 2015). Contrary to popular belief, scavenging is a widespread strategy across many taxonomic groups (e.g., birds, rodents, carnivores, reptiles, arthropods, etc.), with most predators acting as facultative scavengers (DeVault et al. 2003). Carrion represents a high-quality food resource that can be assimilated efficiently by consumers, meaning scavenger consumption of carrion helps retain nutrient availability in higher trophic levels rather than allowing it to return to the detrital pool. Furthermore, carrion resources may increase consumer population growth rates, which in turn enhances their ability to exert top-down pressure on prey populations and stabilize food webs (Wilson and Wolkovich 2011).

The recent collapse of vulture populations in India following mass accidental poisoning presents a sobering example of how altering scavenging guilds can have cascading impacts on the environment. Vulture declines triggered feral dog (*Canis familiaris*) and rat (*Rattus rattus*) population expansions, ultimately resulting in a human health crisis from increased rabies exposure (Ogada et al. 2012a). Although a few studies have shown significant impacts of anthropogenic activities on scavenging dynamics, including altered efficiency (carcass removal) (DeVault et al. 2011, Olson et al. 2012, Huijbers et al. 2013), activity patterns (Huijbers et al. 2015), and shifts in scavenger composition (Tan and Corlett 2012, Huijbers et al. 2015, Sebastian-Gonzalez et al. 2019), occupancy (Twining et al. 2017), or dominance (DeVault et al. 2011), greater understanding of changes in scavenging dynamics due to anthropogenic disturbances remains a priority (Barton et al. 2013, Beasley et al. 2015).

The Fukushima Exclusion Zone (FEZ) offers a unique opportunity to study how ecosystem processes are impacted by massive shifts in anthropogenic activity. The FEZ was formed as a result of the widespread nuclear contamination released after a 9.0 magnitude earthquake generated a tsunami that damaged the Fukushima-Daiichi nuclear power plant in 2011 (Steinhauser et al. 2014). Almost 120,000 people were evacuated from areas surrounding the power plant (Ohnishi 2011), leaving behind empty homes and other human infrastructure. Although there has been a push for radioecological research to describe the full impacts of radionuclide releases into the environment, few researchers have investigated how anthropogenic aspects of the accident – such as the evacuation of humans – have affected ecosystem processes. Recent work suggests wildlife populations are flourishing in the FEZ despite the presence of nuclear contamination, with some species such as wild boar (*Sus scrofa*) being more abundant inside the FEZ than in the surrounding landscape (Lyons et al. In Press). A similar phenomenon of wildlife thriving in areas where humans have been excluded has also been observed in the Chernobyl Exclusion Zone (IAEA 2006, Deryabina et al. 2015, Webster et al. 2016, Schlichting et al. 2019) and the Korean Demilitarized Zone (Kim 1997, Kim and Cho 2005). Large disturbances such as the 2011 nuclear accident and subsequent human evacuation have the potential to influence ecosystem processes, but evidence of rewilding suggests the lack of human activity can outweigh effects from chronic low-dose radiation. Studying scavenging dynamics in the FEZ will further our understanding of wildlife communities and nutrient flow in a contaminated system, and provide information on ecosystem health and stability.

Although scavenging communities are well-characterized in parts of North America (DeVault et al. 2003, Wilmers and Post 2006, Abernethy et al. 2016, Sebastian-Gonzalez et al. 2019), Europe (Selva et al. 2005, Mateo-Tomás et al. 2015, Paula et al. 2015, Schlichting et al. 2019), and Africa (Jones et al. 2015, Mateo-Tomás et al. 2015, Moleón et al. 2015), less research exists on scavenging dynamics in Asia, particularly in Japan (but see Sugiura et al. 2013, Sugiura and Hayashi 2018). To fill this gap in the literature and provide a basis for understanding ecosystem processes in the FEZ, the objective of our study was to characterize the vertebrate scavenging guild in Fukushima, Japan and test the effect of human habitation, carcass size (Moleón et al. 2015, Turner et al. 2017) and habitat (Turner et al. 2017) on scavenging dynamics. Specifically, we tested the hypotheses that: 1) carcass size and habitat would influence scavenger guild composition and efficiency, 2) larger carcasses would persist longer and have higher scavenger richness, and that 3) scavenging guilds in the FEZ would be equally diverse and efficient as those occurring in surrounding landscape. Our study took place during Japan's rainy season, so we also tested the hypothesis that 4) rain increases carcass detection and persistence time via decreases in temperature and potential suppression of invertebrate and vertebrate scavenging activity (Selva et al. 2005, Paula et al. 2015).

METHODS

Study site

A large portion of the landscape surrounding the Fukushima Daiichi Nuclear Power Plant was evacuated after the accident in March 2011, but beginning in 2016 restrictions have been lifted in portions of that area to allow human repopulation following the decrease of radiation to safe levels (Fukushima Prefectural Government 2019). As of 2017, the FEZ covered approximately 371 km^2 of land where contaminant levels remained too high for human habitation (Fukushima Prefectural Government 2019), and thus had substantially less human activity compared to the surrounding landscape. Our study site consisted of two sampling areas, one inside the FEZ and the other >18 km north of the FEZ where humans were never evacuated, and radiation levels were at or near background levels. Both areas were relatively rural with natural and plantation forests making up more than 75% of the land (the remainder was composed of <10% rice paddy fields, <10% other agricultural fields, and <5% urban areas) (Steinhauser et al. 2014). The landscape was characterized by mountainous terrain with numerous rivers and streams. Valleys were often inhabited and developed for agricultural use such as rice paddies, while hilltops and slopes remained forested. To minimize any effects of elevation or land use on the composition of vertebrate scavengers between our two general study areas (Lyons et al. In Press), we limited our experimental sites to upland locations within the Abukuma Highlands. The mean elevation at our camera sites was 438 m (range: 49 – 754 m). The average temperature during the study period was approximately 22.7 °C (annual average: 13.9 °C), and the annual precipitation for the region was 1,092.5 mm in 2018 (Japan Meteorological Agency 2018).

Experimental design

All scavenging trials were conducted from May 28– July 20, 2018, and were balanced across two carcass sizes (mice, *Mus musculus;* rabbits, *Sylvilagus* sp.), two forest cover types (deciduous broadleaf and evergreen conifer), and two zones with varying levels of human activity (FEZ, reference area). Carcass size is known to influence scavenger composition in some cases (Moleón et al. 2015, Turner et al. 2017), so we used two different carcass sizes to better capture the diversity of vertebrate scavengers in our study area: mice (12.0 ± 1.4 g) and rabbits (1395.7 ± 246.1 g). All carcasses were obtained frozen from Japanese pet food suppliers (Ryoshindo; Kasugai, Aichi, Japan; Tsukiyono farm: Minakami, Gunma, Japan). No “wild-type” (brown) carcass were available in bulk, so all carcass had white pelage. However, as many scavengers detect carcasses primarily via olfactory cues (Shivik and Clark 1997, DeVault and Rhodes 2002, DeVault et al. 2004, Natusch et al. 2017) and because carcass color was consistent across all treatments, we did not expect it to bias our results. Smaller carrion does not persist in the environment as long as larger carcasses and are more frequently usurped by invertebrates and microbes prior to arrival of vertebrate scavengers (Moleón et al. 2015, Turner et al. 2017), so we doubled the number of mouse trials to allow sufficient power for detecting differences in scavenger community and efficiency. We weighed all carcasses prior to use and calculated average weight for both carcass sizes.

We identified 100 unique sites (50 each in the FEZ and reference area) spaced at least 0.5 km apart. We selected sites according to forest type (i.e., deciduous broadleaf and evergreen conifer forest), forest patch size, and locations where we had previously obtained landowner permission for a separate project. We divided sites evenly between deciduous broadleaf (BL) and evergreen conifer (EC) forests using Geographic Information System (GIS) land cover layers in

ArcMap (v10.1) obtained from the Japanese Aerospace Exploration Agency (2011). We conducted 300 scavenging trials (200 mice, 100 rabbit trials) for a total of 50 mouse and 25 rabbit trials per forest type per zone. Each site had three replicate trials (two mice, one rabbit carcass), and only one trial per site was active at any time during the study. After a preliminary screening of results during the field season, we conducted an additional 17 "redo" trials during this same period to account for suspected failed trials, resulting in 317 total trials. To avoid habituating scavengers to trial locations within the same site, we spatially and temporally varied carcass placement for each trial. In addition to shifting subsequent carcasses at least 50 m from previous trial locations at the same site, we allowed a buffer period after placing a carcass (7 days after mice; 14 days after rabbits) before starting a new trial. We also removed any carcass remains after each trial to prevent visual/olfactory cues from biasing subsequent trials. To limit edge effects, we attempted to keep trial locations within the same forest patch and least 25 m from a forest edge or road whenever possible.

To record scavenging events, we placed carcasses in front of Reconyx no-glow, infrared HyperFire PC900 remote sensing cameras (RECONYX, Inc., Holmen, Wisconsin, USA) mounted to a tree roughly 1 m away. We cleared all vegetation around the carcass to allow easy identification of scavengers/carcass fate and avoid accidental camera trigger. We programmed cameras to take a burst of three photos one second apart upon triggering of the motion-sensor, with a refractory period of 1 min. To detect smaller or ectothermic scavengers not reliably captured by the motion-sensor, we also programmed cameras to take a photo every 5 minutes. We monitored mouse carcasses for 5-7 days and rabbit carcasses for 7 days, which was a sufficient period for the carcasses to be scavenged or decomposed. We kept all rabbit carcasses within the camera view by staking them to the ground with metal stakes and non-relaxing snares attached to a hind leg. Mouse carcasses were staked using either a snare placed around the midsection of the mouse or were tied directly to the stake using black sewing thread. We placed carcasses at varying times throughout the day to avoid time-related bias within trials (Huijbers et al. 2013, Moleón et al. 2015).

Analyses

For each carcass trial, we identified all species that visited or scavenged a carcass from remote camera images. A "visit" consisted of a scavenger or non-scavenger species that appeared in the frame but did not interact with the carcass. We defined a scavenging event as any time a vertebrate scavenger consumed or manipulated a carcass (i.e. touching or moving it), with the carcass displaced, diminished, or missing in subsequent photos. Trials where the carcass was suddenly removed with no visible scavenger were classified as "unknown". We processed all photos using the CPW Photo Warehouse to create timestamped detections for each scavenging event (Newkirk 2016). We considered any consecutive photos of a species at the same location within 10 minutes of the previous photo be a single detection. All statistical analyses were performed with program R (v3.4.1) (R Core Team 2017).

Scavenging efficiency

We defined scavenger efficiency as a vertebrate scavenger's ability to locate and consume a carcass. To distinguish between carcasses fully scavenged by vertebrates and those partially scavenged by vertebrates but where invertebrates removed the majority of the carcass, we quantified both 1) the proportion of trials in which the majority of the carcass was removed by a vertebrate scavenger, and 2) the proportion of trials scavenged by a vertebrate (overall scavenging rate, no matter how much of the carcass was consumed). We also recorded the time (in hours) until a carcass was first scavenged (“detection time”) and entirely scavenged or decomposed (“persistence time”).

To test the effects of carcass size, habitat, and zone of human activity on whether or not a carcass was scavenged, we used Generalized Linear Models (GLM) with a binomial error distribution and a logit link. We created models based on a priori hypotheses with combinations of our three main variables and their interactions. We also ran a separate model using only data from mouse carcasses to test if attaching the carcass to the stake via snare or thread had a significant effect on whether a carcass was scavenged.

For analyses of detection time, we included failed trials where the carcass fate was unclear (See Results) as long as the carcass was detected before the trial failed (i.e., we counted trials where the carcass was partially scavenged before it was removed from the frame as “detected”). We used the package “survival” (Therneau and Lumley 2015) in R to calculate the probability of a carcass being detected over time. We used a log rank test to calculate χ^2 for observed and expected events for each time step to evaluate the effects of carcass size, habitat, and human activity zone on detection. To test the effect of rain on carcass detection by vertebrate scavengers, we determined the presence or absence of rain while the carcass was still present by examining the time lapse photos and included the categorical variable rain (yes/no) in our models.

To analyze carcass persistence time, we excluded trials that failed due to camera malfunction or the carcass being removed prematurely before a carcass was fully scavenged or decomposed. When carcass remains (i.e., flesh or hair/bones) were present at the end of the trial period, we assigned the entire length of the trial as the persistence time. Similar to the detection analyses, we used the “survival” package (Therneau and Lumley 2015) in R to calculate the probability of a carcass persisting through time, and cox proportional hazards models to test the effects of carcass size, habitat, human activity zone, and their interactions on persistence time. We also tested for the effects of rain on carcass persistence.

Scavenger species composition

We assessed species composition in three ways across each of our response variables (i.e. zone, habitat, and carcass size): overall species richness, species richness per trial, and the percent occurrence of scavenger species. Overall species richness was a count of the species detected across trials in each combination of the variables zone, habitat, and carcass size. For this analysis we counted overall species richness separately for species observed scavenging as well as all observed species (scavengers and non-scavengers) to characterize the scavenger and general wildlife community composition across our two study areas. We also tested the effects of zone, habitat, and carcass size (and their interactions) on scavenger species richness within each trial. To do so, we ran Generalized Linear Mixed Effects Regression (GLMER) models in R with a Poisson distribution, including "site" as a random effect. To quantify the overall percent occurrence of each scavenger species, we calculated the proportion of trials a species scavenged divided by the total number of trials. We then calculated percent occurrence for scavenger species across each subgroup of variables (e.g., percent occurrence of scavengers for each carcass size in each zone). We recorded the proportion of trials visited but not scavenged by both scavenger and non-scavenger species to get a better understanding of the entire wildlife community. To help characterize each species' role in the scavenging community and identify dominant scavengers, we also calculated the proportion of trials for which each species was the first scavenger ("First Scavenger) and the proportion of carcasses each species fully removed or consumed ("Final Scavenger").

RESULTS

Of the 317 trials, we removed 8 trials completely from all analyses because camera malfunction left us unable to determine carcass fate (scavenged vs. not scavenged). Another 39 trials also experienced camera malfunction or the carcass was removed from the frame. For these cases, we were able to determine whether any scavenging events occurred before the trial failed. We included data from these 39 trials in analyses of carcass fate, detection time, species richness, and percent occurrence of species, leaving roughly similar sample sizes between habitats (BL: 151, CF: 158) and human activity zones (FEZ = 157; reference = 152). After excluding those 39 trials from persistence time analyses (n = 270), sample sizes were still similar between habitats (BL: 136, EC: 134) and zones (FEZ: 138, reference: 132).

Scavenging efficiency

A total of 73.1% of all carcasses were scavenged at least once by a vertebrate, of which 23.6% were partially scavenged and 49.5% were fully scavenged (removed by a vertebrate). Overall scavenging rates varied by carcass size (mouse: 58.9%, n = 209; rabbit: 99%, n = 100), but were similar among habitats (BL: 72.2%, n = 151; CF: 71.5%, n = 158) and human activity zones (FEZ: 72%, n = 157; reference: 72%, n = 152). Our analyses of carcass fate revealed that carcass size ($Z = 4.10$, $p < 0.0001$) had a significant effect on carcasses being scavenged, but not habitat ($Z = -0.91$, $p = 38$) or human activity ($Z = 0.04$, $p = 0.90$). None of the interactions between variables were significant, including human activity x carcass size ($Z = 0.02$, $p = 0.99$), habitat x carcass size ($Z = -0.02$, $p = 0.99$), and habitat x human activity ($Z = -0.41$, $p = 0.64$). The presence of a metal snare on mice carcasses had no effect on whether it was scavenged compared to carcasses attached via thread ($Z = -0.14$, $p = 0.89$).

Carcass Detection

Of the trials where a carcass was detected by a vertebrate before the trial failed or ended (n = 225), the average detection time differed significantly between carcass sizes ($\chi^2_1 = 43.87$, $p < 0.0001$), but not human activity zones ($\chi^2_1 = 3.4$, $p = 0.07$) or habitats ($\chi^2_1 = 0.35$, $p = 0.56$). Mouse carcass detection was 63% faster than rabbit carcass detection, and carcass detection in the reference area was 22% faster than the FEZ (Table 2.2). Although carcasses were detected slightly faster without rain, the effect was not significant ($\chi^2_1 = 3.32$, $p = 0.20$).

Carcass persistence

After removing 47 trials due to failure before a carcass was fully scavenged or decomposed, we used a total of 270 trials (170 mice, 100 rabbit) with known carcass fate for persistence analyses. Twenty-eight rabbit carcasses (28%) and 9 mouse carcasses (4%) had remains present at the end of the trial and were given the trial length (14 or 7 days, respectively) as the persistence time. Persistence time varied by carcass type and whether or not it rained but did not differ between habitat ($\chi^2_1 = 0.37$, $p = 0.54$) or human activity zones ($\chi^2_1 = 0.24$, $p = 0.62$). Rabbit carcasses persisted an average of 71.6 hours longer than mouse carcasses ($\chi^2_1 = 24.55$, $p < 0.0001$). Both carcasses sizes lasted longer if it rained at least once while the carcass was present compared to trials without rain ($\chi^2_1 = 23.82$, $p < 0.0001$) (Fig. 2.4). Mouse carcasses persisted almost twice as long when rain occurred during the trial ($\bar{x} = 61.9$ h, n = 75) than during trials where no rain occurred ($\bar{x} = 31.5$ h, n = 92). Similarly, rabbit carcasses persisted 1.5 times longer when rain occurred ($\bar{x} = 129.4$ h, n = 68 vs. $\bar{x} = 88.9$ h, n = 29).

Community composition

Species richness

Overall, we documented ≥ 20 total species (several taxa such as birds and snakes were not identified to species), of which we documented 13 scavenging (Table 2.1). Species richness was similar but slightly higher inside the FEZ compared to the reference area for all species (19 vs. 16) and scavenger species (13 vs. 11). Mammals were the dominant scavengers (n = 9) in both zones, although we also documented scavenging by avian (n = 2) and reptilian (n = 2) species. The overall number of scavenger species was similar between habitats (BL: 11; CF: 12) and carcass sizes (mouse: 12; rabbit: 13), but the scavenger species richness per trial varied by carcass size. As expected, rabbit carcasses had significantly higher average scavenger richness per carcass than mouse carcasses (2.36 vs. 1.33; $p < 0.0001$), with a maximum of six species scavenging a single carcass. Average scavenger species richness at each trial was not significantly different between habitats (BL: 1.83, CF: 1.74, $p = 0.59$) or human activity zones (FEZ: 1.85, reference area: 1.72, $p = 0.46$).

Percent occurrence

The most common scavenger species among our scavenging trials was the large field mouse (*Apodemus speciosus*), which scavenged at 33.4% of all trials (n = 309). The next three most frequent scavengers were raccoon dog (*Nyctereutes procyonoides;* 26.5%), wild boar (21.4%), and civet (*Paguma lavarta*, 20.4%); the remaining scavengers occurred at less than 10% of all trials. Percent occurrence of scavenger species varied by carcass type for several species (Table 2.1). The most frequent scavenger of mouse carcasses were field mice, while the top scavenger of rabbit carcasses were raccoon dogs. Wild boar, civets, foxes (*Vulpes vulpes*), and jungle crows (*Corvus macrorhynchos*) also scavenged rabbit carcasses more frequently than mouse carcasses.

Percent occurrence of scavenger species also varied by human activity zone for some species (Fig. 2.1). Wild boar scavenged more frequently in the FEZ, scavenging 27.4% of all FEZ trials but only 16.4% of reference area trials. Mice scavenged 35.7% of all FEZ trials, but only 28.9% of reference area trials. Although we didn't document any scavenging activity by Japanese macaque (*Macaca fuscata*) or Japanese hare (*Lepus brachyurus*), they also visited more frequently in the FEZ (macaque: 9.6% vs. 2.6%; hare: 19.7% vs. 7.9%). Other species showed the opposite trend. For example, Japanese serow (*Capricornis crispus*) visited more carcasses in the reference area (20.4% vs. 2.5%), and snakes scavenged and visited more carcasses in the reference area than the FEZ (5.9% vs. 1.3%).

Some species visited carcasses at a much higher rate than they scavenged, such as mice, marten (*Martes melampus*), and shrew-mole (*Urotrichus talpoides*) (Table 2.1). Although field mice visited approximately 80% of all carcasses, they scavenged at 38.7% of mouse and 16% of rabbit trials. In contrast, raccoon dogs and civets both visited and scavenged roughly 50% of rabbit carcasses but visited and scavenged 10% or less of mouse carcasses, presumably because rabbit carcasses were larger and less likely to be removed by invertebrates before scavengers could detect them.

First scavenger

Of the carcasses scavenged, large field mice were the first scavenger at a surprisingly high percentage of mouse carcasses (62.4%), followed by wild boar (12.0%), and then civet and raccoon dog (both 7.2%). For rabbit carcasses, the most common first scavengers were civet (24.5%), raccoon dog (22.4%), mice (14.3%), and boar (12.2%). Given that mice were common scavengers but unable to fully consume rabbit carcasses in our study, we also removed scavenging events by mice and reanalyzed the data to investigate the most common first scavenger species other than mice. From these analyses, the most frequent first scavengers of mouse carcasses were wild boar (25.8%), raccoon dog (22.7%), and civet (16.7%), whereas the first scavengers of rabbit carcasses were raccoon dog (30.2%), civet (28.1%), crow (13.5%), and wild boar (12.5%). Some species showed differences between zones: both foxes and snakes were more likely to be the first scavengers at rabbit carcasses in the reference area than the FEZ, whereas raccoon dog and civet showed the opposite pattern (Fig. 2.2).

Final scavenger

Field mice were the dominant final scavenger of mouse carcasses, removing 30.2% of mouse carcasses removed by vertebrates, but did not completely consume any rabbit carcasses due to the disparity in size. Instead, mice scavenged easily accessible parts of rabbit carcasses such as the face, ears, appendages, and anus. The final scavenger of rabbit carcasses was most frequently a raccoon dog (29%) or wild boar (26%) (Fig. 2.3), because these two species were strong enough to consistently remove an entire rabbit carcass by pulling it free from the snare or yanking the stake from the ground. Although more species were observed scavenging at rabbit carcasses than mouse carcasses (11 vs. 12 spp.), the smaller size of mouse carcasses enabled them to be fully removed by a greater diversity of scavengers (10 vs. 6 spp.) than rabbit carcasses.

The proportion of trials removed by each scavenger species was similar across both forest types but differed by zone and carcass size (Fig. 2.3). Together, wild boar and raccoon dogs removed 68% of all rabbit carcasses in the FEZ but only 42% in the control zone, where more rabbit carcasses were either taken by foxes or not fully removed by any vertebrate scavenger before the trial ended (52%). Invertebrates removed roughly 50% of mouse carcasses in each zone, and the remainder of mouse carcasses were removed by scavenger species in similar proportions in each zone—except for field mice and boar. Wild boar removed five times more mouse carcasses in the FEZ than the control area (20.5% vs. 4.3%), whereas field mice removed almost twice as many mouse carcasses in the control area than the FEZ (25.0% vs. 39.0%).

DISCUSSION

Despite the presence of radiological contamination, vertebrate scavengers inside the FEZ were equally as diverse and efficient as in the surrounding landscape. Approximately 70% of all carcasses were scavenged by 13 species in the evacuated FEZ and 11 species in the inhabited reference area. Mammals were the dominant scavengers in this study, making up 69% of the scavenger species and removing 50% of all carcasses, although we also documented avian and reptilian scavengers. Carcass size rather than habitat or human activity zone significantly influenced scavenger community composition, species richness per carcass, and persistence time, but we did observe slight differences in scavenging rates between zones for a few species. In particular, wild boar exhibited increased scavenging rates and carcass removal in the FEZ compared to the inhabited reference area, likely reflecting differences in the abundance of this species between zones (Lyons et al. In Press). Our results suggest a diversity of scavengers in the FEZ, which may contribute to the functional redundancy and stability of the ecosystem. High scavenging rates indicate some ecosystem services such as carcass removal have not been negatively impacted by the 2011 nuclear accident. By characterizing the scavenging community in the FEZ, we also provide potential pathways of nutrient and radionuclide distribution in a radiologically contaminated ecosystem.

Overall, carcass size affected scavenging dynamics more than habitat or human activity zone. As we hypothesized, larger rabbit carcasses persisted longer and were more likely to be scavenged by a greater number of vertebrate species (Moleón et al. 2015, Olson et al. 2016, DeVault et al. 2017). In addition to scavenging at more rabbit than mouse carcasses, mesocarnivores spent more time at rabbit carcasses and we recorded several instances of inter- and intra-specific interactions between individuals fighting for dominance of carrion resources. Carcass size also strongly affected scavenger community composition in that small carcasses increased the ability of smaller scavengers (i.e., rodents, snakes) to physically remove carcasses. Although mouse carcasses were detected faster due to their rapid decomposition and the corresponding release of olfactory cues (Jojola-Elverum et al. 2001, DeVault et al. 2003), the smaller size enabled invertebrates to remove mouse carcasses at higher rates prior to detection or removal by vertebrate scavengers (Abernethy et al. 2017). Carrion beetles frequently buried mouse carcasses within a matter of hours after placement, thus monopolizing them as vertebrate scavengers rarely located mouse carcasses after they were underground. The high rate of invertebrate scavenging indicates intense competition with vertebrate scavengers for carrion resources that increases the functional redundancy of carcass removal services (Beasley et al. 2015, Sugiura and Hayashi 2018).

Most aspects of scavenging dynamics were comparable across zones, including the proportion of carcasses scavenged, carcass persistence time, and scavenger species richness. The lack of difference in overall scavenging rates and persistence is likely due to similar abundances of mesocarnivores scavengers (i.e., raccoon dog and civet) in the FEZ and reference area (Lyons et al. In Press). The high diversity and efficiency of scavengers in both zones indicate the scavenging communities are functionally redundant, which enhances the ecosystem's capacity to withstand disturbances and provide ecosystem services by increasing the complexity of the food web (Wilson and Wolkovich 2011, Mori et al. 2013). We found no evidence that scavengers in the inhabited reference area were negatively affected by human activity, likely because the landscape was sufficiently rural with enough forested land cover to support similar populations of mesocarnivores (Lyons et al. In Press). However, there were subtle differences in some species-specific scavenging rates that may have implications for nutrient distribution within the food web. The overall proportion of carcasses scavenged was equal between zones, so increased scavenging rates and abundance of wild boar in the FEZ may result in boar monopolizing carrion resources that would otherwise be used by other species. Interestingly, more rabbit carcasses were removed by foxes or not fully scavenged by the trial's end in the reference area where wild boar are much less abundant (Lyons et al. In Press). We also observed more snakes visiting and scavenging carcasses in the reference area, and although the reason is unclear, it may be related to land use changes such as rice paddy abandonment following the evacuation (Matsushima et al. 2015, Kidera et al. 2018). The higher scavenging rates of foxes and snakes seemed to drive the faster detection of rabbit carcasses in the reference area, as both species were more likely to find rabbit carcasses first in the reference area than in the FEZ. Overall, however, the scavenging community composition and efficiency was similar between the FEZ and inhabited reference area.

Spatial aspects of carcass placement and the vegetation structure surrounding carrion can substantially influence carcass availability to potential scavengers as well as alter avian scavenger behavior (Roen and Yahner 2005, Smith et al. 2017, Pardo-Barquín et al. 2019). The relatively low scavenging rates by avian scavengers (2.5%) in this study were likely due to our placement of carcasses in forest interiors. Sugiura and Hayashi (2018) noted similarly low scavenging rates of mouse carcasses by carrion crow (*Corvus corone*) from forest floors in western Japan. Although birds' ability to fly may aid in detecting carrion resources faster than terrestrial scavengers, this benefit may be limited to more open habitats where they can spot carcasses from afar (Ruxton and Houston 2004, Ogada et al. 2012b, Pardo-Barquín et al. 2019), particularly for species that forage primarily via visual cues (Byrne et al. 2019). Most mammalian and reptilian scavengers detect carcass via olfaction and thus have an advantage in finding carcasses in forests compared to avian scavengers, many of which rely primarily on vision (Shivik and Clark 1997, DeVault and Rhodes 2002, DeVault et al. 2004). The larger size and longer persistence time of rabbit carcasses may have enabled crows to locate them on forest floors easier than mouse carcasses, resulting in higher proportions of rabbits scavenged by crows in this study.

We predicted habitat would impact scavenger species richness or efficiency of carcass removal given its documented effect on scavenging dynamics (Selva et al. 2005, Abernethy et al. 2016, Abernethy et al. 2017, Turner et al. 2017, Pardo-Barquín et al. 2019), but we were unable to detect differences between deciduous broadleaf forests and evergreen conifer forests. Sugiura et al. (2013) observed similar carcass removal rates between natural deciduous forests and conifer plantations in Japan, indicating the two forest types supported similar vertebrate and invertebrate scavenging communities. The effects of habitat on scavenging communities are complex and moderated by interactions with carcass size (Turner et al. 2017) and spatial scale, as both landscape and local habitat characteristics influence scavenging communities (Saito and Koike 2013, Pardo-Barquín et al. 2019). Our classification of forest types used large-scale spatial data and we did not quantify the vegetation structure and microhabitat characteristics within our field sites; thus it is possible the two forest types evaluated in this study may have been more alike than the land covers compared in other scavenging studies (e.g., forested vs. open) (Selva et al. 2005, Lim 2015, Abernethy et al. 2016). Any differences in vegetation structure between the two forests may not have been drastic enough to affect the accessibility or detection of carcasses by mesocarnivores that rely primarily on olfactory cues. Furthermore, habitat can also influence scavenging dynamics through the role it plays in species abundance via factors like habitat selection and availability of food resources (Tsujino and Yumoto 2014, Abernethy et al. 2016), but scavengers were likely not restricted to a single forest type in our study given the home range size of many mesopredators and the mosaic nature of the landscape in our study area (Saito and Koike 2013).

Rodents were the first vertebrates to detect and scavenge carcasses at a surprisingly large proportion of trials (30%), more so than any other scavenger. The presence of mice at 80% of both mouse and rabbit trials across all zones suggests they are widespread and common in the area (Kubota et al. 2015). The higher density of rodents relative to mesocarnivores or boar likely increased the probability that a mouse would find and scavenge a carcass before it was removed by invertebrates or scavenged by other vertebrates (Paula et al. 2015). Several studies have observed scavenging by rodents by using remote cameras (Bumann and Stauffer 2002, DeVault and Rhodes 2002, Young et al. 2014, Paula et al. 2015, Abernethy et al. 2016), but fewer have documented rodents the most frequent/dominant scavenger (Schlichting et al. 2019). Our data suggest the functional role of rodents as scavengers may be understated in the literature due to difficulties in detection with motion-activated cameras, because the combination of their small size and the variation in camera quality and set-up between studies makes reliably detecting rodents problematic. Our use of 5-minute time lapse photos substantially increased our ability to detect scavenging by field mice even when they didn't trigger the camera's motion sensor—including multiple mice simultaneously feeding at the same carcass. The time lapse settings also captured several instances of scavenging behavior (n = 11) by ectothermic reptiles that otherwise would have gone undetected by motion-triggered cameras. For example, several snakes attempted to scavenge rabbit carcass, frequently biting and coiling around the rabbit's face despite the carcass being much larger than the snake. Our detection of snakes via only time lapse photos helps illustrate why snakes have traditionally been underestimated as scavengers (DeVault and Krochmal 2002), despite the widespread prevalence of scavenging behavior across snake species (Shivik and Clark 1997, Golla and Durso 2015, Pandirkar et al. 2015, Natusch et al. 2017, Smith et al. 2017, Ucha and Santos 2017).

It is possible the carcasses' white pelage may have inflated scavenging rates in this study by enabling easier detection of carcasses. However, while scavenging rates were generally high during this study, they were within the range reported in the literature, including previous studies conducted using mouse carcasses in Japan (47-58%; Sugiura et al. 2013, Sugiura and Hayashi 2018 vs. 58% in this study) and in North America using "wild-type" mice during the warm-season (45-63%; DeVault et al. 2011, Olson et al. 2012). Furthermore, most facultative scavengers detect carcasses primarily via olfactory cues (Shivik and Clark 1997, DeVault and Rhodes 2002, DeVault et al. 2004, Natusch et al. 2017), and thus pelage color likely plays little role in detection of carrion by terrestrial scavengers.

Collectively, our data suggest that carcass size had a greater effect on scavenging dynamics than habitat or human activity. Carcass size played a major role in determining carcass detection and persistence as well as the allocation of carrion resources to vertebrate and invertebrate scavengers. Another interesting result from this study was the occurrence of rain during trials increased the persistence time of carcasses considerably, regardless of carcass size. Although the effects of rain on carcass persistence aren't well-studied, some studies have suggested precipitation may prolong carcass decomposition by decreasing vertebrate and invertebrate activity, or interfering with olfactory cues that lead to carcass detection by vertebrate scavengers (Campobasso et al. 2001, Selva et al. 2005, Paula et al. 2015). Detection by vertebrate scavengers was slightly but not significantly reduced by the occurrence of rain in this study, possibly because factors like windspeed, humidity and the amount and duration of rainfall also impact detection but were not measured (Ruzicka and Conover 2012). Additionally, rain is closely linked to temperature, which influences scavenging efficiency and carcass persistence (DeVault et al. 2004, DeVault et al. 2011, Turner et al. 2017). Future research to clarify the interaction between temperature and precipitation, and how it influences invertebrate activity and detection by vertebrate scavengers, would increase our understanding of carcass persistence across seasons and climates.

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Table 2.1: Proportion of all experimentally placed carcasses (n = 309) visited and scavenged by all species across both carcass sizes (mice, rabbits) in the Fukushima Exclusion Zone (FEZ) and inhabited reference area in Fukushima, Japan from May – July 2018.

Species	Percentage of visited carcasses (%)		Percentage of scavenged carcasses (%)	
	Mouse (n = 209)	Rabbit (n = 100)	Mouse (n = 209)	Rabbit (n = 100)
Mammalian				
Large field mouse (*Apodemus specious*)	**80.9 (169)**	**81.0 (81)**	**40.2 (84)**	16.0 (16)
Wild boar (*Sus scrofa*)	20.1 (42)	31.0 (31)	10.0 (21)	45.0 (45)
Raccoon dog (*Nyctereutes procyonoides*)	10.5 (22)	49.0 (49)	9.1 (19)	**63.0 (63)**
Masked palm civet (*Paguma lavarta*)	11.5 (24)	46.0 (46)	5.7 (12)	51.0 (51)
Japanese red fox (*Vulpes vulpes*)	1.4 (3)	7.0 (7)	0.5 (1)	15.0 (15)
Japanese marten (*Martes melampus*)	15.3 (32)	21.0 (21)	1.0 (2)	4.0 (4)
Japanese shrew-mole (*Urotrichus talpoides*)	7.7 (16)	3.0 (3)	1.0 (2)	0.0 (0)
Japanese badger (*Meles anakuma*)	7.2 (15)	10.0 (10)	0.0 (0)	0.0 (0)
Raccoon (*Procyon lotor*)	0.0 (0)	0.8 (1)	0.0 (0)	1.0 (1)
Domestic dog (*Canis lupus familiaris*)	0.0 (0)	0.8 (1)	0.0 (0)	1.0 (1)
Domestic cat (*Felis catus*)	2.4 (5)	3.0 (3)	0.0 (0)	0.0 (0)
Japanese weasel (*Mustela itatsi*)	1.0 (2)	1.0 (1)	0.0 (0)	0.0 (0)
Japanese hare (Lepus brachyurus)	16.7 (35)	8.0 (8)	0.0 (0)	0.0 (0)
Japanese squirrel (*Sciurus lis*)	11.5 (24)	6.0 (6)	0.0 (0)	0.0 (0)
Japanese serow (*Capricornis crispus*)	11.0 (23)	12.0 (12)	0.0 (0)	0.0 (0)
Japanese macaque (*Macaca fuscata*)	8.1 (17)	2.0 (2)	0.0 (0)	0.0 (0)
Avian				
Black kite (*Milvus migrans*)	0.5 (1)	1.0 (1)	1.4 (3)	1.0 (1)

Jungle crow (*Corvus macrorhynchos*)	1.4 (3)	4.0 (4)	1.9 (4)	21.0 (21)
Pheasant*	11.5 (24)	4.0 (4)	0.0 (0)	0.0 (0)
Bird (other)*	5.7 (12)	9.0 (9)	0.0 (0)	0.0 (0)
Reptile				
Japanese rat snake (*Elaphe climacophora*)	1.0 (2)	5.0 (5)	1.4 (3)	6.0 (6)
Burrowing rat snake (*Euprepiophis conspicillata*)	1.4 (3)	1.0 (1)	0.5 (1)	1.0 (1)
snake (other)*	2.9 (7)	4.0 (4)	0.0 (0)	0.0 (0)
Unknown	6.2 (13)	6.0 (6)	5.3 (11)	8.0 (8)

*Not identified to species

Table 2.2: Mean time and standard deviation (SD) in hours until carcasses were first detected (i.e., scavenged) across habitats, carcass sizes, and human activity zones in Fukushima, Japan. FEZ= Fukushima Exclusion Zone; BL = deciduous broadleaf; EC = evergreen conifer.

Zone	**Habitat**	**Carcass Size**							
		Mouse				**Rabbit**			
		Mean ± SD (h)	**Min (h)**	**Max (h)**	**n**	**Mean ± SD (h)**	**Min (h)**	**Max (h)**	**n**
FEZ	**BL**	18.54 ± 27.79	0.59	157.75	34	60.16 ± 33.39	5.58	118.52	25
	EC	25.37 ± 41.47	0.57	181.38	30	58.53 ± 45.38	1.38	132.06	25
Reference	**BL**	14.58 ± 16.73	1.11	59.17	30	49.24 ± 28.76	12.41	107.30	25
	EC	21.15 ± 22.38	2.75	106.14	32	42.90 ± 37.21	2.50	132.08	24

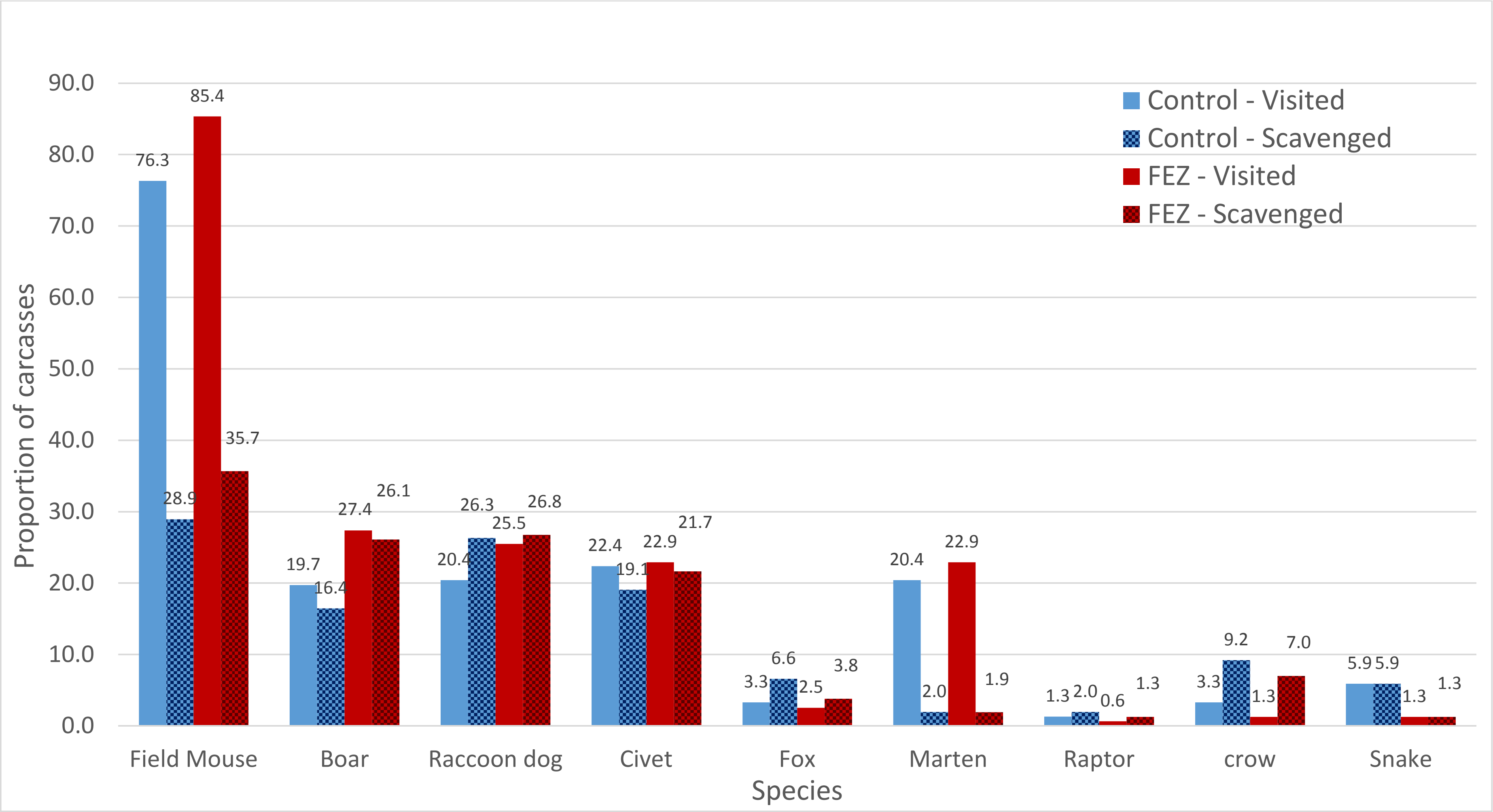

Figure 2.1: Proportion of experimentally placed carcasses (n = 309) scavenged by common scavenger species in the Fukushima Exclusion Zone (FEZ) and inhabited reference (control) area during May – July 2018. Proportion of carcasses visited (but not scavenged) is also provided for reference.

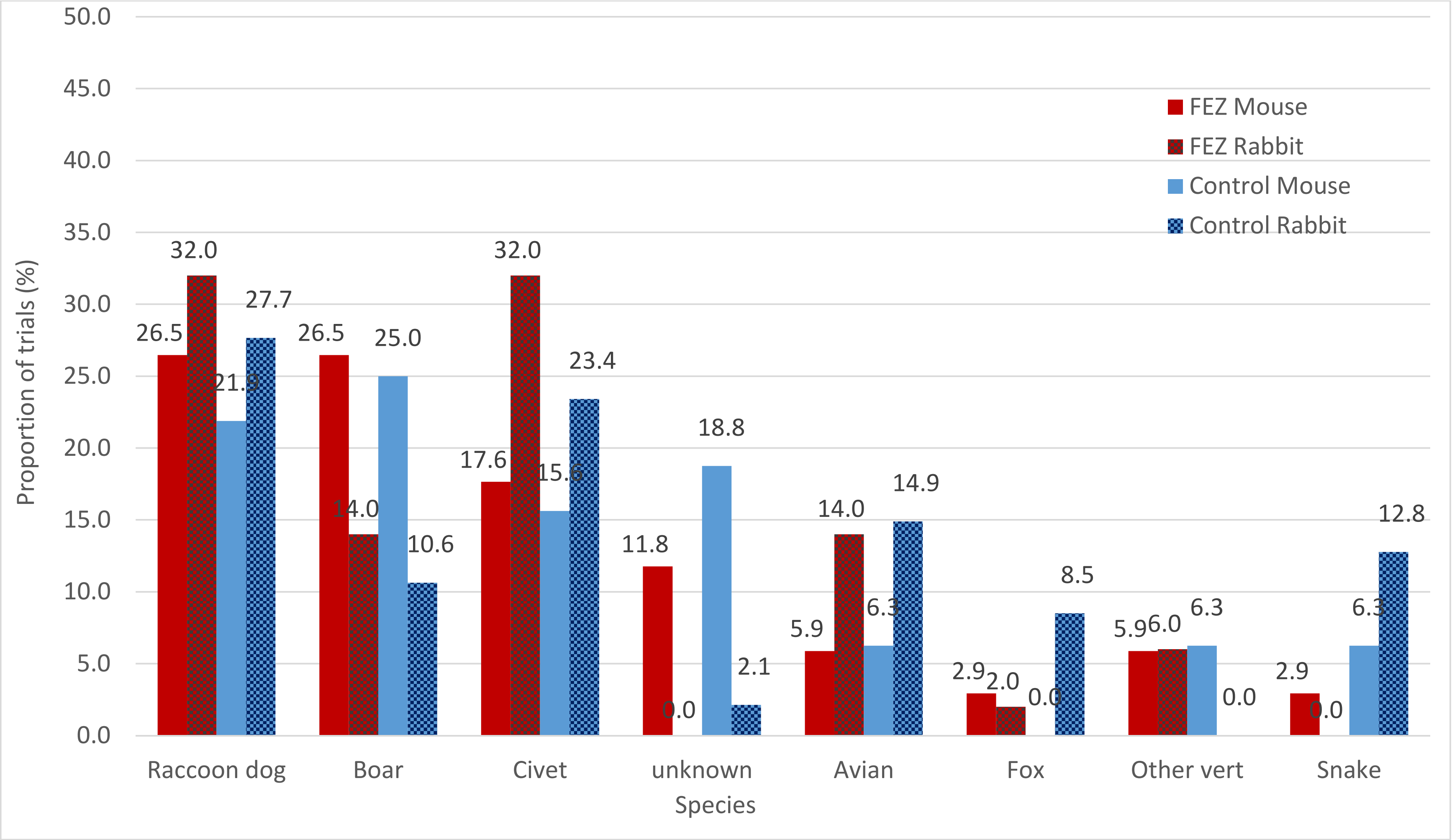

Figure 2.2: Proportion of experimentally placed rabbit and mouse carcasses (n = 163) at which each species was the first scavenger (not including scavenging events by mice to allow further analysis of scavenging patterns) in both the Fukushima Exclusion Zone (FEZ) and inhabited reference (control) area during May to July 2018.

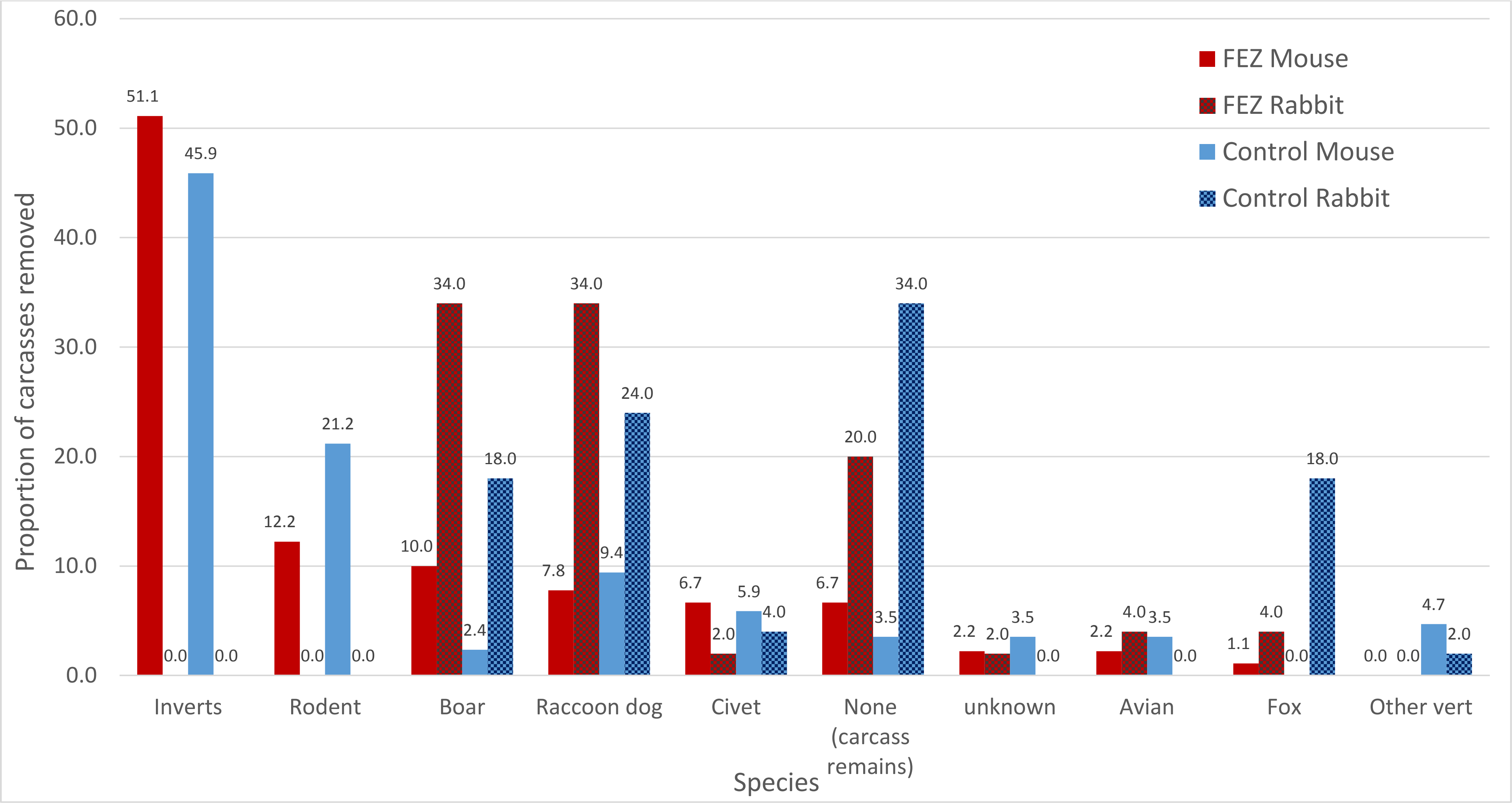

Figure 2.3: Proportion of experimentally placed rabbit and mouse carcasses (n = 275) fully removed by vertebrate scavenger species or invertebrates in both the Fukushima Exclusion Zone (FEZ) and inhabited reference (control) area during May to July 2018.

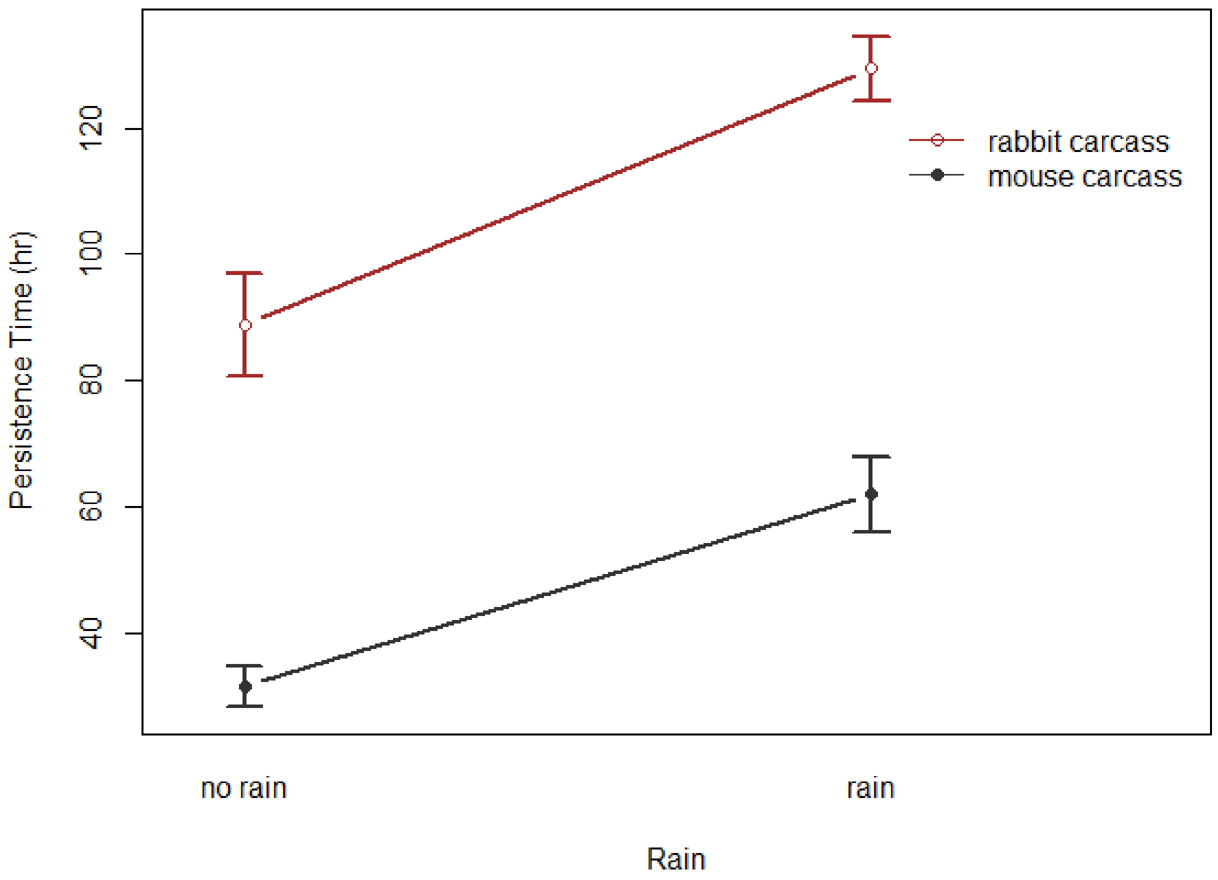

Figure 2.4: Mean time in hours (with confidence intervals) until carcasses (n = 270) were fully scavenged or decomposed with and without rain during the experimental trials. Mean persistence time for both rabbit and mouse carcasses are displayed.

CHAPTER 3

MOVEMENT BEHAVIOR AND HABITAT SELECTION OF SNAKES (*ELAPHE* SPP.) IN THE FUKUSHIMA EXCLUSION ZONE

Gerke, H.C., T.G. Hinton, and J.C. Beasley. Submitted to Copeia, August 15, 2019.

ABSTRACT

The 2011 nuclear accident in Fukushima, Japan was one of the largest anthropogenic releases of radioactive contamination in history, and many questions remain regarding its ecological impacts. As part of a larger study estimating animal movements and radiation exposure within the impacted area, we used a combination of VHF and GPS transmitters to estimate home range size and habitat selection of nine Japanese rat snakes (*Elaphe climacophora* and *E. quadrivirgata*) over three months within the Fukushima Exclusion Zone. Short-term aLocoH ranges varied from 0.15-6.80 ha, and daily movements ranged from 30-116 m. Snakes appeared to be primarily diurnal with longer movements during daylight hours. Short-term home ranges included more areas close to streams, buildings, and roads, as well as more grassland and less evergreen forest than expected given the availability of these habitat components on the landscape. Within their home ranges, snakes used areas close to streams and avoided evergreen broadleaf forests. They also frequently used habitat features such as trees and buildings, although use of buildings was highly variable among individuals. The limited movement rates of snakes compared to more mobile species suggests snakes could be useful bioindicators of local contamination, but radionuclide exposure likely varies considerably among individual snakes within localized areas due to differences in arboreal habitat use and overall habitat selection.

INTRODUCTION

On 11 March 2011, a 9-magnitude earthquake struck off the northeastern coast of Japan, damaging the Fukushima Daiichi Nuclear Power Plant and resulting in one of the most significant releases of anthropogenic radiological contamination in history. Humans were evacuated from a 1,150 km^2 area surrounding the site, and in many cases populations of wildlife have responded favorably to the absence of humans from the landscape (Lyons et al. In Press).

Similar wildlife responses occurred within the Chernobyl Exclusion Zone (IAEA 2006, Deryabina et al. 2015, Webster et al. 2016, Schlichting et al. 2019). However, wildlife are exposed to chronic low-dose radiation with unknown biological effects (IAEA 2006, Hinton et al. 2007, Hinton et al. 2013, Stark et al. 2017). Consequently, studies to determine impacts of radiation exposure to wildlife are a high priority (Hinton et al. 2013). Such determinations are often challenging as environmental contamination can be heterogeneously distributed across the landscape, and thus an animal's exposure to contaminants depends on life history characteristics such as diet, home range size, and habitat selection (Chesser et al. 2000, Congdon et al. 2001, Stark et al. 2004, Stark et al. 2017). As a result, basic natural history information on habitat use and movement is needed to better inform models of exposure and dose estimation (Gaines et al. 2005, Purucker et al. 2007, Hinton et al. 2015).

Unlike many species of birds and large mammals, reptiles and amphibians often exhibit high site fidelity and have small home ranges, making them useful organisms for assessing uptake patterns and biological effects of contaminant exposure across landscape contamination gradients (Hopkins 2000, Leaphart et al. 2019). As strict carnivores and scavengers of animal carcasses (DeVault and Krochmal 2002, Campbell et al. 2012, Dorcas et al. 2012, Steen et al. 2014, Smith et al. 2017), snakes may be particularly prone to accumulating contaminants (Brisbin et al. 1974, Campbell and Campbell 2001, Fuma et al. 2017). Japanese rat snakes (*Elaphe climacophora* and *E. quadrivirgata*) are abundant within the Fukushima Exclusion Zone (FEZ) and some aspects of their ecology necessary for measuring radiation exposure, including diet, are well-studied (Mori 1991, Tanaka 2007, Mori and Vincent 2008, Mori and Nagata 2016). Nonetheless, a key knowledge gap for Japanese rat snakes needed to understand and estimate radiation exposure patterns is their spatial ecology. Such data are needed to elucidate potential mechanisms contributing to the high radionuclide levels, as dose rates can vary across land cover types and forest edges (Koarashi et al. 2016, Imamura et al. 2018). Japanese rat snakes are known to be common near streams and houses (Fukada 1978, Mori and Nagata 2016), and from studies of other rat snake species in North America, we know some snakes utilize forest edges for foraging or thermoregulation (Durner and Gates 1993, Blouin-Demers and Weatherhead 2001b, Row and Blouin-Demers 2006b), habitat selection can differ relative to spatial scale (Sperry and Weatherhead 2009, Hoss et al. 2010, Martino et al. 2012), and human disturbance may influence movement rates (Parent and Weatherhead 2000, Sealy 2002, Beale et al. 2016).

The objectives of this study were to use GPS and VHF radio telemetry to quantify 1) short-term home range sizes, 2) daily movement rates and activity times, and 3) habitat use patterns for Japanese rat snakes (*E. climacophora* and *E. quadrivirgata*) at multiple spatial scales within the FEZ. We expected rat snakes to be primarily diurnal (Mori 1989, Fukada 1990), that rat snake habitat use would vary across spatial scales due to changes in habitat availability or selection for habitat components at different scales (i.e., macro- or microhabitats) (Harvey and Weatherhead 2006), and snakes would select habitat features such as streams, edges, buildings, and roads (Fukada 1978, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001b, Row and Blouin-Demers 2006b, Mori and Nagata 2016). We included roads due to their association with buildings and potential role in thermoregulation by retaining heat (Lelièvre et al. 2010, McCardle and Fontenot 2016). Throughout the paper we make comparisons to new world rat snakes due to the lack of published work on Japanese rat snake movement ecology. Despite recent taxonomic changes that no longer assign them the same genus (Utiger et al. 2002), we argue they are remain functionally similar in their habits, behavior, and diet.

METHODS

Study Site

Within the FEZ, we focused our research within the Abukuma Highlands, ~25 km northwest of the Fukushima Daiichi Nuclear Power Plant. The average temperature during the study period was approximately 22.7 °C (annual average: 13.9 °C), and the annual precipitation for the region was 1,092.5 mm in 2018 (Japan Meteorological Agency 2018). The terrain was hilly with numerous streams and rivers and an elevation range of 270-790 m (mean: 504 m). The landscape was rural prior to the accident, primarily characterized by deciduous hardwood forests, coniferous plantations, grassland, abandoned rice paddies and farmland, and abandoned residential and municipal areas. Empty homes, farms, and other human-made structures remained scattered across the landscape. People were prohibited from residing in the FEZ and human activity in our study area was minimal with the exception of the occasional presence of workers engaging in decontamination efforts along roads.

Telemetry

We collected snakes by hand via opportunistic encounters on roads and brought them back to the Institute of Environmental Radioactivity (IER) for transmitter attachment and processing. All handling techniques were in accordance with IACUC approval (protocol A2015 12-017-Y3-A6) and the Animal Use Committee of Fukushima University. We fitted snakes >80 cm snout-vent length (SVL) with rechargeable UHF/GPS transmitters (~4 g, Alle 60, Ecotone Telemetry, Poland) attached externally to the dorsolateral surface via duct tape and super glue far enough down the snakes' bodies so as not to increase their maximum circumference. After placing an initial piece of tape around the snakes' body, we superglued the transmitter to the tape rather than scales. We then covered the transmitter with another strip of tape to prevent snagging. To facilitate tracking, we also attached a VHF transmitter (~1g, BD-2, Holohil Systems Ltd., Ontario, Canada) in the same manner after ensuring the cumulative weight of both GPS and VHF transmitters was no more than 5% of the snakes' mass. We retained all snakes overnight in the laboratory to allow them to acclimate to the transmitters and we released them at their capture location the following day. We programmed the GPS to collect location data every hour, with fixes supplemented by behavioral observations of snake activity via manual VHF tracking when possible (~4 times/week). GPS transmitter batteries had a lifespan of 1-2 weeks, and thus we located snakes every 24-72 hours to collect additional locational observations, download data from the transmitters, and recapture individuals as necessary to recharge transmitters. At the end of the study, we recaptured the snakes and removed their transmitters.

Prior to deployment on snakes, we quantified accuracy of GPS transmitters by deploying them in open and forested land covers within the study region. To calculate transmitter error, we took the average distance from all points to the known GPS coordinates and ran a one-way ANOVA to test for differences between land covers. We also calculated the average proportion of successful fixes for each stationary GPS unit to compare against fix rates obtained from GPS transmitters on snakes.

Home Range and Movements

We performed all home range analyses in R (v3.4.1) with the adehabitatHR package using Minimum Convex Polygon (MCP) and Adaptive Local Convex Hull (a-LoCoH) home range estimators. Although there are short-comings to this approach (Powell 2000, Pattishall and Cundall 2008), we generated 95% MCP home range estimates to allow for comparison with previous studies due to its traditional use, and because some authors recommend MCP for reptile home range estimates or smaller sample sizes (Row and Blouin-Demers 2006a, Boyle et al.

2009). MCP home range estimates were not used in selection analyses. We also derived 95% home range estimates using adaptive LoCoH due to its ability to produce ranges with hard edges and represent linear movements without overestimating the used area (Getz et al. 2007). The a-LoCoH method uses a sphere with a variable radius around a point to decide the neighboring points used to construct local hulls, with the sum of the distances to neighboring points being less than or equal to "*a*". We based the "*a"* parameter on the maximum distance between any two points in a snake's dataset and visually evaluated the output according to the ''minimum spurious hole covering'' (MSHC) rule, where the smallest value of "*a*" that covers spurious holes is selected (Getz et al. 2007). GPS points that were obviously influenced by error were not included in any analyses (as determined by unrealistic distance from previous/subsequent GPS points and verified VHF relocations). To test if home range size was influenced by the number of GPS/VHF points collected among individuals, we ran a linear regression for both the 95% MCP and a-LoCoH ranges.

We also estimated the average daily distance moved and daily activity patterns of snakes using GPS points only. We estimated the daily distance moved by averaging the distance between the closest successful fix to noon on each subsequent day for each snake. Only fixes within six hours of noon were included. To examine differences in activity throughout the day, we calculated the distance between all consecutive GPS points for each snake and categorized them as day (05:00-19:00) or night (19:00-04:59) based on sunrise/sunset times. We used a one-way ANOVA to test for differences in the average distance between all diurnal and nocturnal relocations. We also quantified average movement distances per hour to elucidate temporal peaks in activity.

Habitat Selection

We defined habitat as described by Hall et al. (1997): “the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism”. We used Wides resource selection analyses (Calenge 2011) in R with the package adehabitatHS to quantify habitat selection at two spatial scales: population and home range (Johnson’s second and third order selection; Johnson 1980). We included land cover as well as distance to the nearest road, building, stream, and edge as variables in the analyses, with edge defined as the boundary between an open and forested area (Blouin-Demers and Weatherhead 2001b). We obtained high-resolution (10 x 10 m) land cover data (Japan Aerospace Exploration Agency 2011) that consisted of the following categories: deciduous hardwood, deciduous softwood, evergreen broadleaf, evergreen conifer, grassland, rice paddy, urban, upland (crop), bare land, water, and snow and ice. After comparing the land cover database to satellite imagery and conditions on the ground, we reclassified several land covers. Bare and upland (crop) were infrequent and patchy, and strongly associated with the urban category; thus, we combined these land cover types into a new category called “rural”. Similarly, we merged rice paddy and grassland as the two were often indistinguishable due to lack of paddy maintenance after the FEZ was evacuated. All other covariates were created as rasters in ArcGIS (v10.1) by calculating distance to existing vector data (roads, streams, etc.). Continuous variables were delineated into the following distance categories: 0-50, 50-150, 150-250, >250 m.

For population-scale selection analyses, because snakes were roughly clustered in two areas, we created a 100% MCP around all snake relocations in each cluster from which to derive habitat availability data. We buffered these polygons by the maximum distance traveled by any snake during the study period (estimated with GPS points), and the resulting combined area was considered the available habitat for all snakes (Fig. 3.1). We generated 3,434 random points (twice as many points as VHF locations and successful GPS locations across all individuals) throughout the available habitat area to represent estimates of availability among our covariates. These values were contrasted against covariate values similarly extracted for each snake GPS/VHF relocation to test for selection at the population scale. We performed similar analyses at the home range scale, where we extracted covariate values from GPS/VHF relocations and compared them to those generated from random points (twice as many random points as relocations per individual) created within each snake's 100% a-LoCoH range. We used the proportion of points in the available and used areas to generate average selection ratios using WidesII and WidesIII analyses (Calenge 2011). For each measured habitat attribute, use was considered different from availability if 95% confidence intervals of the average selection ratio did not overlap the value of one. To determine significant differences between categories (e.g., between two land cover types), we assessed the Bonferroni-corrected 95% confidence interval on the difference of the selection ratios between categories. Pairings with intervals overlapping the value of zero were considered not different.

In addition to our GPS-based habitat selection analyses, we also were interested in the extent to which tracked snakes used abandoned buildings and tree canopies. To quantify snake use of these habitat features, we recorded the number and percentage of snakes observed at least once in trees and buildings based on VHF relocation observations.

RESULTS

Home range and Movements

We recorded 1,616 GPS locations and 102 VHF locations from nine snakes (eight *E. climacophora*, one *E. quadrivirgata*) comprised of six females and three males. Snakes were tracked from 10 - 28 days from 16 June to 1 August 2018, and the number of relocations ranged from 40 - 424 ($\bar{x}$ = 191 ± 118) among individuals. One snake lost its GPS transmitter after two days and was not included in movement analyses (calculated from GPS points only), but it was tracked via its VHF transmitter and is included in home range and habitat selection analyses. The average fix rate for stationary GPS transmitters used to measure error was 97.36%, slightly higher than that of the transmitters on snakes (86.70%). The average error for stationary transmitters was 46 ± 67 m, and there were no significant differences ($P > 0.05$) in error between land covers (average number of points per land cover = 179).

Our analysis examining the influence of the number of points on snake home range size revealed a significant relationship for the 95% a-LoCoH estimator ($P < 0.01$, $t = 3.87$, $r^2 = 0.64$), but not 95% MCP ($P > 0.05$, $t = 1.808$, $r^2 = 0.22$). After excluding the two snakes with the fewest points ($n = 40$, $n = 44$), the relationship for the a-LoCoH estimator was no longer significant; however, due to our limited sample size we report home ranges for all snakes and included all individuals in habitat selection analyses. Short-term 95% a-LoCoH ranges varied from 0.25 - 6.59 ha, with an average area of 2.77 ± 1.94 ha and average maximum width of 342 ± 204 m (Table 3.1). The average 95% short-term MCP range was 6.40 ± 4.72 ha (range: 0.89 - 11.99 ha), over twice as large as estimated a-LoCoH ranges. After excluding the two snakes with less than 50 relocations, average 95% a-LoCoh and MCP ranges were 3.48 ± 1.53 ha and 7.95 ± 4.14 ha, respectively, with an average maximum a-LoCoH range width of 352 ± 187 m.

The average daily distance traveled (calculated from GPS points; excluding one individual that lost its GPS after two days) was 64 ± 33 m. Within a day, snakes typically moved short distances between points, with an average distance moved of 49 ± 42 m, and 90% of all snake movements were under 104 m in length. These estimates include GPS error and thus are likely overestimates of actual movements. Snakes also appeared to be more active during the day, as the average distance between points was 15 m greater during the day than at night (F_1 = 47.06, P < 0.001) (Fig. 3.2).

Habitat Selection

At the population scale, all snakes showed selection for land cover attributes. Although the selection ratio for rural developed areas was three times higher than any other land cover type, there was extensive variation among individuals as half the snakes strongly selected rural developed areas and the other half avoided them (Fig. 3.3). On average, snake home ranges had significantly higher than expected proportions of grassland (abandoned rice paddy) and significantly less evergreen conifer and evergreen broadleaf than available at the population scale. Snakes also selected areas within 50 m of streams, roads, and edges, and within 50-150 m of buildings (Fig.3.4).

Among land cover types, on average snakes used land cover in proportion to its availability within their home range, except for evergreen broadleaf, which was avoided similar to the population scale (Fig. 3.5). Evergreen conifer followed a similar trend of avoidance at both scales, but the confidence interval slightly overlapped one (CI = 0.04 - 1.01). As observed at the population scale, snakes also used areas within 50 m of streams more frequently than expected within their home range (Fig. 3.4). Snakes appeared to select areas more proximate (within 50 m) to roads (although this confidence interval also overlapped one, CI = 0.9842 - 1.4707), and avoided areas over 250 m from roads, with only one point recorded >250 m from a road. Despite avoiding distances further from buildings and edges, snakes didn’t select for proximity to either one within their home ranges. Nevertheless, all snake points except for a few from one individual occurred within 150 m of an edge, and none were over 180 m from the nearest edge.

Although we were not always able to record specific behaviors during VHF tracking due to snakes frequently being out of sight (e.g., under vegetation or not visible within the tree canopy), all but two snakes were seen climbing or resting in trees (n = 7, 78%) (Supplemental Figure 1). However, one individual not observed in a tree during the study took refuge on the second floor of an abandoned building, necessitating climbing to get there. Overall, 5 snakes took refuge in a building (56%), with some individuals entering multiple structures.

DISCUSSION

This is the first study to describe home range size, movements, and habitat selection in Japanese rat snakes - notably within the landscape abandoned after the Fukushima Daiichi nuclear accident. As expected, we found rat snake habitat selection differed slightly across spatial scales, but snakes consistently avoided evergreen broadleaf and evergreen conifer forests while selecting areas proximal to streams. Snakes were more active and moved further during daytime, although they often remained in the same retreat for multiple days, resulting in relatively small average movements and home ranges. Collectively, these data provide valuable insight into snake movement rates, behavior, and habitat selection within a contaminated landscape that will better inform future estimates of external radiation exposure and ultimately reduce uncertainties of dose-effect relationships for snakes in the FEZ.

Snakes in our study limited their use of evergreen conifer and avoided evergreen broadleaf land cover at both spatial scales. Evergreen conifer within the study area consisted primarily of Japanese cedar plantations (*Cryptomeria japonica*), and no snakes were observed using this land cover while manually tracking. The deep litter, sparse undergrowth, and lower plant diversity may result in less desirable vegetation structure compared to other available land covers within the landscape (e.g., less camouflage, cover, or climbing opportunities that influence predation risk or foraging success). Similarly, evergreen broadleaf areas were commonly dense bamboo (*Phyllostachys* sp.) or dwarf bamboo (*Sasa* sp.) thickets, which may not offer efficient thermoregulatory opportunities due to low light conditions on the ground (Oshima 1961). Vegetation structure may also drive habitat selection patterns by encouraging selection of habitat components that minimize energy loss while enabling predation success (Mullin and Cooper 2000). Thus, snakes may have avoided evergreen broadleaf forests as dense vegetation structure can obscure visual cues from prey. For example, Mullin et al. (1998) found a habitat's structural complexity can influence predation success, with gray rat snakes experiencing decreased success in areas with barren or highly complex vegetation structure.

Selection of grassland at the population scale by snakes tracked in our study may be explained by its association with several different interspersed land cover types that form a heterogeneous mosaic, offering high prey diversity and thermoregulatory opportunities. Snakes used more grassland than expected given its availability on the landscape, with most grassland consisting of abandoned rice paddies transitioning through secondary succession. These small rice paddies were often near former residences and roads and were bordered by streams or irrigation ditches. The proximity of abandoned paddies, roads, streams, and forest edges may explain why snakes selected disproportionately more area near these features compared to the overall landscape. The interspersion of previously human-associated areas (paddies, orchards/farmland) and forested hills creates a heterogeneous landscape suitable for many species (Katoh et al. 2009), including snakes. This mosaic of habitat components could benefit snakes by providing varied prey opportunities. In addition to providing high prey diversity, neighboring patches with structurally different vegetation establish a gradient of microhabitats ideal for moderating body temperature without expending energy to move far distances (Blouin-

Demers and Weatherhead 2001b). Thermoregulation is considered one of the most important factors influencing habitat use in temperate terrestrial reptiles (Blouin-Demers and Weatherhead 2001a, Lelièvre et al. 2011), and could be driving snake selection for habitat characteristics at the population scale.

Subtle or unapparent selection patterns within the home range suggest individual snakes in our study may have optimized home range placement at broader spatial scales. The lack of selection for specific land cover types within the home range may also reflect the generalist behavior of rat snakes, which have been found in numerous vegetation types (Fukada 1978, Goris and Maeda 2004, Hirai 2004, Hamao 2005a). Alternatively, if Japanese rat snakes don't select specific land cover types during the warmer seasons but exhibit selection during cooler periods for hibernacula, seasonal differences in selection patterns could expand the home range area and influence habitat selection results found in this study at both scales (Sperry and Weatherhead 2009).

The high selection ratios for rural land cover and areas close to buildings at the population scale suggests human structures could be important for snakes, but we observed extensive differences in use among tracked individuals. Variation in individual habitat use and movement has been widely documented among snakes (Macartney et al. 1988, Sperry and Weatherhead 2009, George et al. 2015) and may complicate identification of space use patterns. However, despite the lack of selection for proximity to buildings within home ranges, over half of the snakes used human structures during the study. Two snakes shed their skin after retreating to buildings and several live snakes or skins were observed around the same buildings, suggesting multiple inhabitants and/or a habitual retreat for shedding (Porter and Czaplicki 1974). Buildings and associated anthropogenic features (e.g., wood and trash piles, collapsed roofing, greenhouse tarps, etc.) could provide shelter from predators during the vulnerable period surrounding shedding when snake visibility and movements are reduced (Porter and Czaplicki 1974, King and Turmo 1997), in addition to benefits such as refugia for thermoregulation and habitat for mammalian prey (Blouin-Demers and Weatherhead 2002, Lelièvre et al. 2010). Although we did not monitor snake movements within human-inhabited areas, as an endotherm specialist, *E. climacophora* could benefit from the increase in abandoned buildings and reduced human activity within the FEZ.

Our expectation that snakes would select edges at the home range scale given the importance of edge habitat to other snakes (Durner and Gates 1993, Blouin-Demers and Weatherhead 2001b, Row and Blouin-Demers 2006b) was not supported. Japanese rat snakes may select for heterogeneous areas that provide close access to different vegetation types rather than the transitional vegetation between land cover types. Another possibility for the lack of edge selection during the warm season is that temperatures remained benign enough for areas of average thermal quality to permit sufficient thermoregulation (Carfagno and Weatherhead 2006, Tanaka 2007). However, we suspect the lack of apparent edge selection was due to our edge definition (i.e., boundary of forest/open land cover data), which does not reflect variation in microhabitat and vegetation structure that snakes may select for at finer scales.

Vegetation structure may be important for Japanese rat snakes, as we observed extensive use of trees, particularly around streams. The lone tracked *E. quadrivirgata* resided entirely along the banks of a small stream bordering an abandoned paddy, supporting previous observations of foraging in streams for frogs that often represent their primary prey (Mori et al. 1992, Hirai 2004, Mori and Nagata 2016). Although generally described as terrestrial, this snake was observed climbing a small tree and regularly rested on vines and vegetation. Mori et al.

(1992) also recorded *E. quadrivirgata* using trees to opportunistically ambush treefrogs. Consistent with other reports (Goris and Naganuma 1979, Mori and Nagata 2016), several *E. climacophora* tracked during our study were also frequently observed along streams, with one individual spending its time primarily within a riparian corridor (often in trees). Our observations support the semi-arboreal nature of *E. climacophora* (Fukada 1978, Eguchi 1980, Hamao 2005), although the proportion of time spent in trees appeared to vary among individuals.

Overall, snake movement rates appeared low and resulted in small short-term ranges. Although we tried to minimize disturbance while tracking, it's possible frequent relocations and occasional recaptures influenced snake behavior. Individuals often remained within roughly 10 m of the same point for multiple days before moving distances of around 50-150 m over a few days to another refuge—although arboreal movement within trees could underestimate movements as our GPS transmitters were unable to accurately account for vertical movements made by climbing snakes. As expected, snakes moved further distances during daylight hours and appeared to be primarily diurnal. Field observations and prey-handling experiments indicate Japanese *Elaphe spp.* are visually oriented predators (Ota 1986, Mori 1990, Mori and Nagata 2016) that actively search for prey (Eguchi 1980, Hamao 2005), so foraging in daytime would offer the best visibility and thermoregulatory benefits for an active predator. We can't discount nighttime snake activity (see Mori et al., 1992), but nocturnal movement rates are probably lower than our data suggest because these estimates include GPS error (i.e., distances between GPS fixes influenced by error imply movement even when a snake remains stationary).

Wildlife inhabiting the FEZ and other areas where anthropogenic radionuclides are present are exposed to varying radiation depending upon diet, behavior, and the spatial distribution of contamination across vegetation types. For example, dose rates in the FEZ are higher at forest edges as well as in evergreen conifer forests compared to deciduous hardwood forests (Koarashi et al. 2016, Imamura et al. 2018). Further, individuals residing primarily in trees lessen their exposure to contaminated soil (Ishida 2016), potentially decreasing heath impacts. Compared to other animals such as birds or large mammals that can travel multiple kilometers per day, limited movement rates of snakes suggest their contaminant burdens should more closely reflect localized radiation levels in their surroundings, meaning snakes could be useful indicators of local environmental contamination. However, given the variable use of land cover attributes as well as arboreal habitat among tracked snakes, our study suggests there is likely considerable heterogeneity in radionuclide exposure among individual snakes within localized areas. Future research should aim to clarify the link between snake movement, external radiation exposure, and radionuclide accumulation to inform assessments of health effects of chronic radiation exposure, and aid in the refinement of radiation exposure models for wildlife inhabiting contaminated environments.

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Table 3.1: Description of nine rat snakes (*Elaphe* spp.) tracked in summer 2018 within the Fukushima Exclusion Zone in Fukushima, Japan, including ID, species, sex, snout-vent length (SVL), length and dates of tracking period, number of GPS and VHF relocations, and 95% home range characteristics using both Minimum Convex Polygon and adaptive Local Convex Hull home range estimators.

ID	Species	Sex	SVL (cm)	Tracking period	Days with active GPS	VHF Locations	Total relocations (GPS + VHF locations)	MCP 95% range area (ha)	a-LoCoH 95% range area (ha)	a-LoCoH range width (m)
EEC6	E. climacophora	F	96.8	June 16 - July 9	9	11	143	5.73	3.38	352.95
EEC7	E. climacophora	M	111.5	June 29 - July 16	12	10	159	8.35	3.22	383.91
EEC16	E. climacophora	M	115.0	June 29 - July 27	22	17	424	11.96	6.60	702.02
EEQ8	E. quadrivirgata	M	81.2	June 30 - July 26	22	12	265	2.34	1.64	217.91
EEC20	E. climacophora	F	98.5	July 06 -July 31	18	15	245	3.54	2.61	252.03
EEC26	E. climacophora	F	127.0	July 13 - July 30	17	12	185	11.99	3.63	627.22
EEC25	E. climacophora	F	85.0	July 13 - July 30	2	12	40	0.89	0.25	136.15
EEC28	E. climacophora	F	111.0	July 14 - July 26	5	7	44	1.03	0.28	110.05
EEC31	E. climacophora	F	100.0	July 20 - August 1	11	6	212	11.72	3.31	297.20

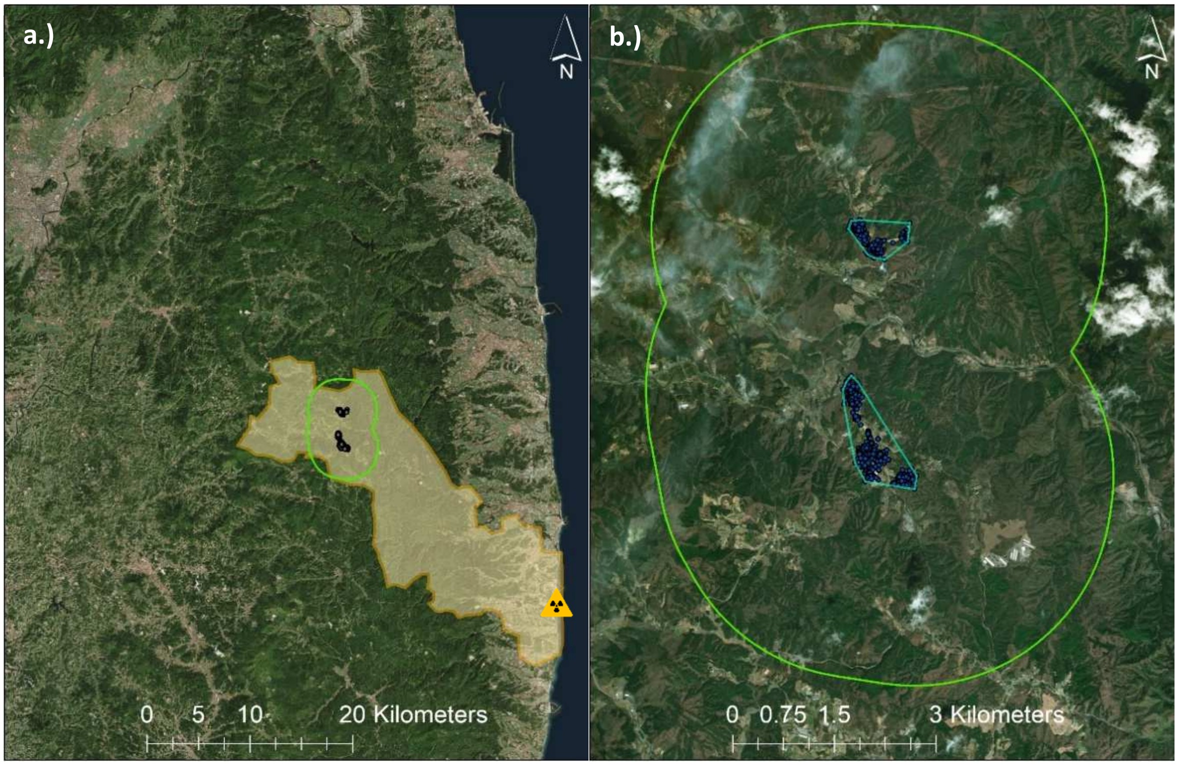

Figure 3.1: a) Map of the evacuated Fukushima Exclusion Zone (FEZ) in yellow in relation to the Fukushima Daiichi Nuclear Power Plant (FDNPP) on the northeastern coast of Japan (gold triangle), with Fukushima city visible in the top left corner. b) Habitat selection for Japanese rat snakes (*Elaphe* spp.) at the population scale was calculated by comparing habitat characteristics at random points generated in the available habitat (light green) to characteristics at snake VHF and GPS relocations (n = 1,717) collected June to August 2018 (dark blue). The available habitat was created by buffering the 100% Minimum Convex Polygon around all snake relocations (light blue) by total distance traveled by a snake over the course of the study period.

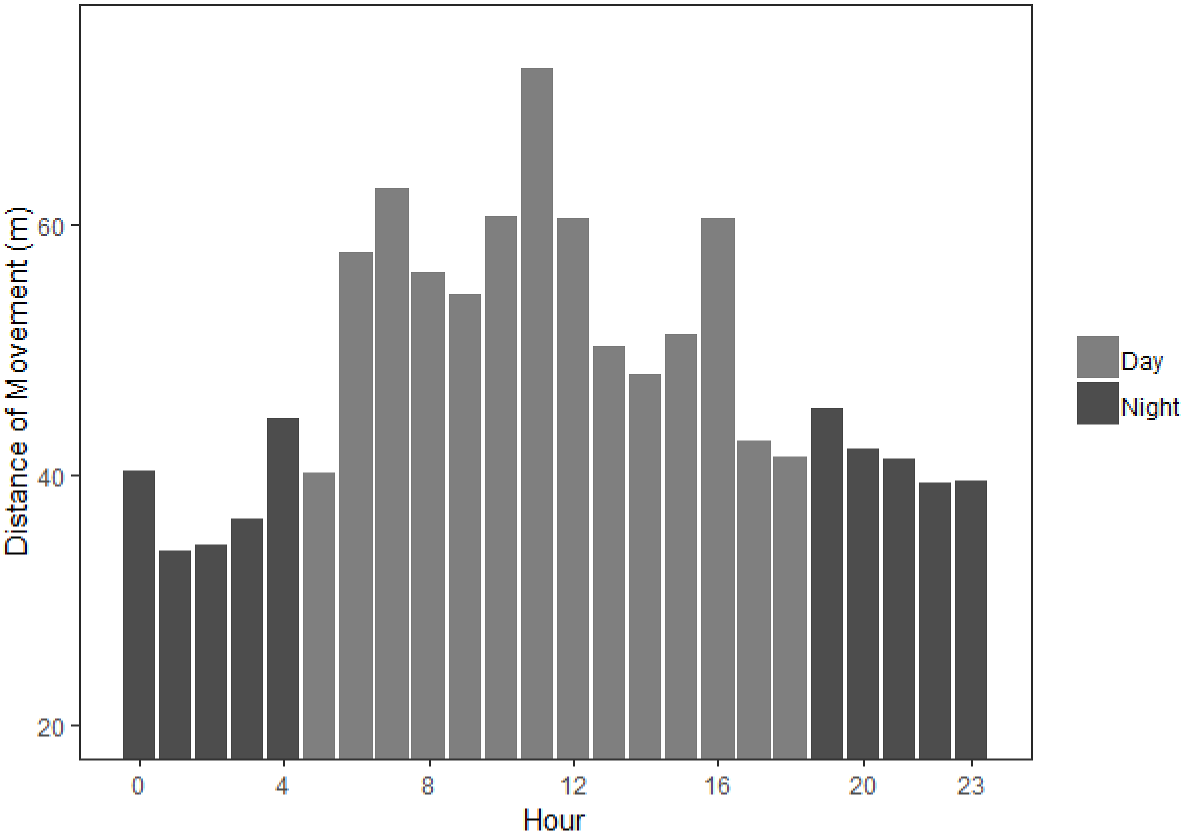

Figure 3.2: Average distance between GPS relocations (n = 1,616) for nine rat snakes (*Elaphe* spp.) tracked June to August 2018 within the Fukushima Exclusion Zone in Fukushima, Japan. Distance between relocations are plotted by hour.

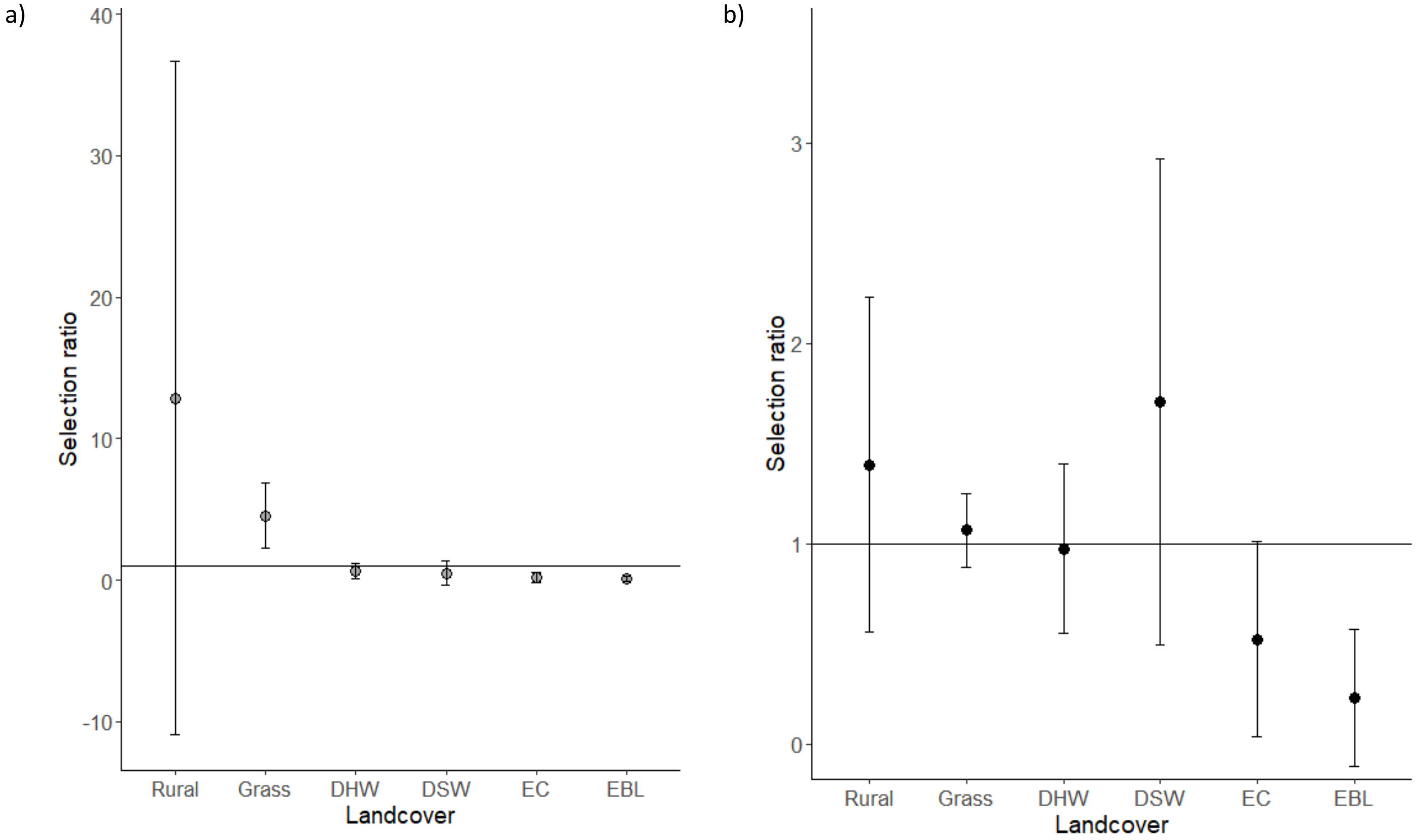

Figure 3.3: Average selection ratios and confidence intervals for land cover types at the a) population scale and b) home range scale, derived from 1,717 relocations from nine rat snakes (*Elaphe* spp.) tracked June to August 2018 within the Fukushima Exclusion Zone in Fukushima, Japan. Land cover types include Rural - rural developed areas including buildings and open areas; Grass - grassland, including abandoned rice paddies; DHW - deciduous hardwood; DSW - deciduous softwood; EC - evergreen conifer; and EBL - evergreen broadleaf. Note differing y-axis scales.

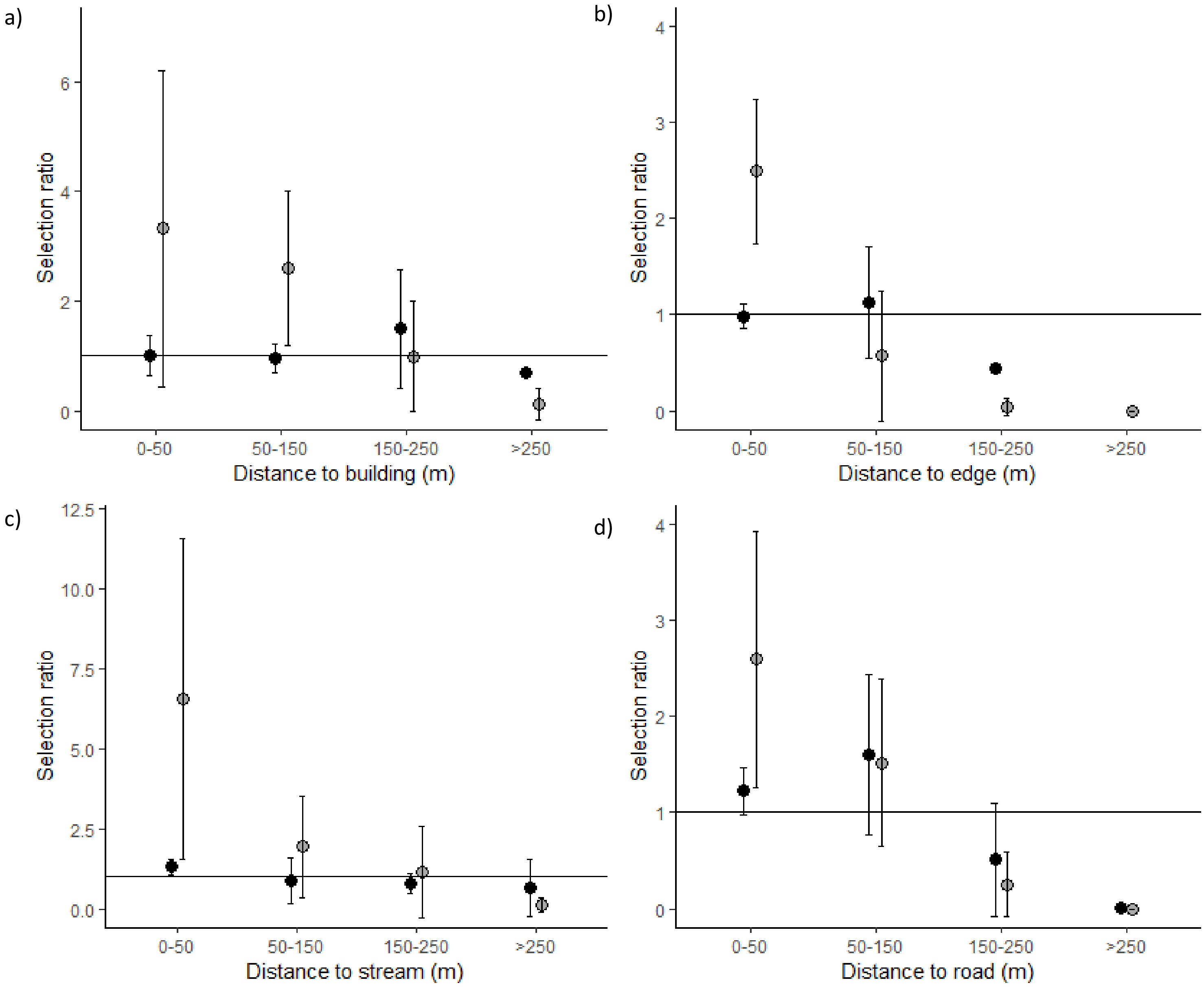

Figure 3.4: Average selection ratios for a) distance to building, b) distance to edge, c) distance to stream, and d) distance to road. Selection ratios were derived from 1,717 relocations from nine rat snakes (*Elaphe* spp.) tracked in June to August 2018 within the Fukushima Exclusion Zone in Fukushima, Japan. Gray points represent selection ratios at the population scale; black points represent the home range scale. Note differing y-axis scales.

Figure 3.5: Example of a Japanese rat snake (*Elaphe climacophora*) with VHF transmitter (left) and GPS transmitter (right).

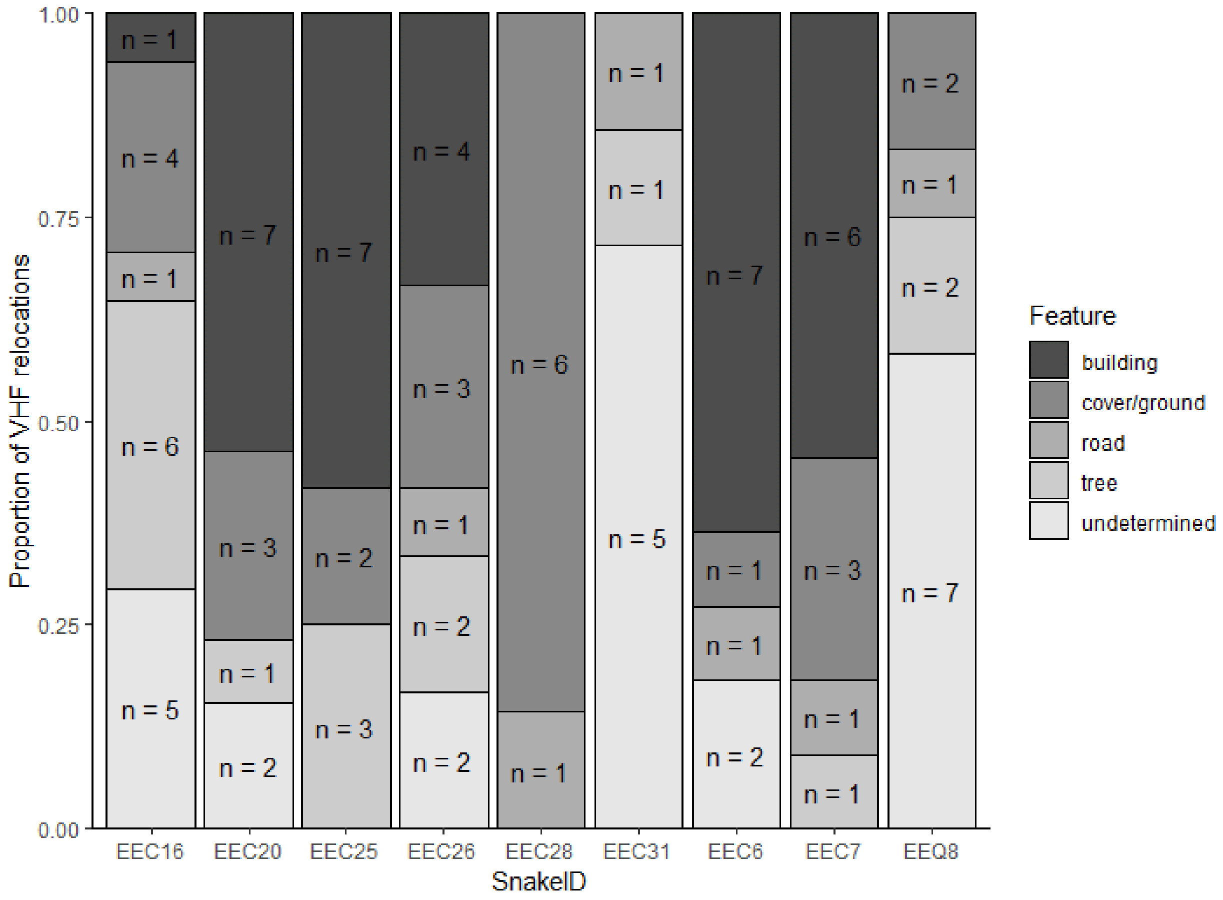

Figure 3.6: Proportion of VHF relocations (n = 102) associated with each habitat feature for all nine rat snakes (*Elaphe* spp.) tracked in June to August 2018 within the Fukushima Exclusion Zone in Fukushima, Japan. Relocations where the snake wasn't visually located and/or could not be pinpointed were classified as undetermined.

CHAPTER 4

DOSE ESTIMATES AND RADIOCESIUM ACTIVITY CONCENTRATIONS IN SNAKES FROM FUKUSHIMA, JAPAN

Gerke, H.C., T.G. Hinton, D.A. Anderson, T. Takase, K. Nanba, and J.C. Beasley. To be submitted to Environment International.

ABSTRACT

Despite being one of the largest anthropogenic releases of radioactive contamination in history, many questions remain regarding the ecological impacts of the 2011 nuclear accident in Fukushima, Japan. In particular, despite their high trophic status, limited home range sizes, and close association with soil, where many radionuclides accumulate, few studies have investigated radiocesium accumulation in snakes. Here we present one of the most comprehensive radioecological studies of snakes to date. We used a combination of whole-body radiocesium analyses, GPS transmitters, and optically-stimulated luminescence (OSL) dosimeters to study rat snakes (*Elaphe* spp.) in the Fukushima Exclusion Zone (FEZ) in Japan. Our objectives were to 1) quantify whole-body radiocesium activity concentrations across several common species of snakes, 2) determine the effects of species, sex, and body size on radiocesium activity concentrations, 3) estimate internal and external dose rates using the ERICA assessment tool, 4) calculate external dose from OSL dosimeters deployed on snakes in contaminated areas, 5) quantify differences in external dose estimates generated via ERICA's default parameters and estimates informed by site-specific soil samples; and 6) test the hypothesis that incorporating snake behavior into exposure models would improve estimates of external dose rates. Whole-body radiocesium levels for snakes were highly variable among individuals (16 to 24,726 Bq/kg, FW) but influenced more by local contamination than species, sex or size. Using ERICA's default concentration ratio resulted in external dose estimates with three times as much variation and underestimated dose received by 73% of the dosimeters placed on tracked snakes, compared to dose estimations informed by soil samples from snake home ranges. The average total dose rate for snakes captured in the FEZ was 3.8 μGy/h, with external dose contributing over 70% to the total dose. Doses recorded by OSL dosimeters on snakes as well as modeling in ERICA

suggest that individual movements and behavior have substantial influence on dose rates to snakes.

INTRODUCTION

Following the nuclear accidents at the Chernobyl and Fukushima Daiichi power plants, there has been a surge of interest in determining the effects of chronic low-dose radiation to humans, wildlife, and other biota (Hinton et al. 2013, Bréchignac et al. 2016, Stark et al. 2017, Beresford et al. 2019). Such assessments require detailed knowledge of an individual's radiation exposure, yet despite advances in technology, large uncertainties remain in our ability to accurately estimate radiation doses for many species (Stark et al. 2017, Anderson et al. 2019, Hinton et al. 2019). One complicating aspect of dose estimations is that the total radiation dose an organism is exposed to is comprised of a combination of internal and external dose, each of which is influenced by a myriad of factors.

Internal dose rates occur through ingestion of radioactive material (radionuclides) that either pass through the gastrointestinal track or are incorporated into the organism's tissues. Uncertainties associated with internal dose rates are increased by variation in age, diet, uptake and accumulation rates, the state of equilibrium between radionuclides in the organism and its surroundings, as well as measurement methods (Forseth et al. 1998, Malek et al. 2004, Ishii et al. 2017, Stark et al. 2017, Nemoto et al. 2018). An organism's external dose is primarily influenced by its exposure to radionuclides in the environment, which are heterogeneously distributed across the landscape (Koarashi et al. 2016, Imamura et al. 2017, Kato et al. 2018). Potential exposure to contaminants can vary substantially among individuals and species across the landscape due to differences in movement behavior and habitat use (Hinton et al. 2015, Imamura et al. 2017, Aramrun et al. 2019), but despite this variability, factors like species-specific movement behavior and space use are often unaccounted for in risk assessments or estimation of external dose rates (Gaines et al. 2005, Stark et al. 2017, Hinton et al. 2019).

Dose estimates are often calculated using computer simulation software (e.g., ERICA; Environment Risk from Ionising Contaminants Assessment and Management) that incorporate data available on radionuclide activity concentrations in the organism (Brown et al. 2008, Brown et al. 2016a), but these estimates are often associated with large uncertainties due to the natural variabilities discussed above, as well as reliance on default parameters generated from limited data sources. Relatively few dosimetry studies have tried to estimate external dose rates, and most that do primarily rely on external dose conversion factors based on soil contamination levels, which can result in inaccurate predictions over large spatial resolutions (Anderson et al. 2019). A small but growing number of studies are attempting to account for uncertainties in wildlife dose estimations by comparing estimated external doses to absorbed dose from dosimeters placed in the environment (Stark and Pettersson 2008, Fuma et al. 2015, Kubota et al. 2015) or on animals (Chesser et al. 2000, Beresford et al. 2008, Hinton et al. 2015, Aramrun et al. 2019, Hinton et al. 2019). However, placing dosimeters on free-ranging animals has only been attempted for some taxa (e.g., mammals, birds, fish), and research on wildlife in radiologically contaminated areas in general is unbalanced across taxa. Although there is a varying degree of radioecological research on mammals (e.g. Deryabina et al. 2015, Kubota et al. 2015, Beresford et al. 2016, Lyons et al. In Press), birds (e.g. Fukasawa et al. 2017, Saito et al. 2019), amphibians (e.g. Fuma et al. 2015, Matsushima et al. 2015, Takahara et al. 2015, Tagami et al. 2018), fish, (e.g. Woodhead 1973, Fukushima and Arai 2014, Wada et al. 2016) and invertebrates (e.g.Yoshioka et al. 2015, Tamaoki 2016, Ishii et al. 2017), research regarding the effects of contaminants on reptiles is especially limited despite repeated calls to address this literature gap (Hopkins 2000, Campbell and Campbell 2001;2002). Basic information necessary for evaluating dose effects – such as radionuclide activity concentrations, radionuclide transfer, and dose estimates – remain scarce or missing for reptiles (Wood et al. 2010, Wood et al. 2012), and for snakes in particular.

Although traditionally understudied compared to other vertebrates, snakes exhibit several traits that make them vulnerable to contaminants, such as small home ranges, site fidelity, longevity, and high trophic status (Hopkins 2000, Campbell and Campbell 2001;2002). Additionally, physiological processes of poikilothermic reptiles are distinct from those of other taxa, causing differences in metabolism, contaminant uptake/accumulation, and biological half-life that may necessitate different toxicity thresholds for some contaminants and influence whole-body activity concentrations (Staton et al. 1974, Campbell and Campbell 2002, Beresford and Wood 2014). For radiocesium – one of the most common, long-lasting radionuclides remaining in many radiologically contaminated areas – only a handful of reports on activity concentrations or dose rates are available for snakes. Most of these data have been collected from the Savannah River Site (SRS) in the United States (Brisbin et al. 1974, Staton et al. 1974, Bagshaw and Brisbin Jr 1985, Brown et al. 2016b), with a few specimens from Chernobyl (Barnett et al. 2009, Oskolkov et al. 2011) and one from Fukushima (Fuma et al. 2017). Brisbin et al. (1974) found snakes to have the highest radiocesium concentration of any naturally occurring vertebrate predator reported at the time, suggesting snakes could accumulate high levels of radiocesium.

Using snakes collected from areas of variable contamination levels in Fukushima, Japan, this study is the first to provide a comprehensive examination of radiocesium activity concentrations and dose estimates informed by GPS transmitters and dosimeters placed on snakes. Our objectives were to 1) quantify whole-body radiocesium activity concentrations across several common species of snakes, 2) determine the effects of species, sex, and body size on radiocesium activity concentrations, 3) estimate internal and external dose rates using the ERICA assessment tool, 4) calculate external dose from OSL dosimeters deployed on snakes in contaminated areas, 5) quantify differences in external dose estimates generated via ERICA's default parameters and estimates informed by site-specific soil samples, and 6) test the hypothesis that incorporating snake behavior into exposure models would improve estimates of external dose rates.

Given that snakes are high trophic-level predators with small home ranges and are often in proximity to contaminated soil, we anticipated snakes would accumulate high levels of radiocesium, but that variation in diet would result in significantly different activity concentrations between snake species (Brisbin et al. 1974). We expected external dose to contribute more than internal dose to the total dose rate (Kubota et al. 2015, Tagami et al. 2018) given the relatively slow metabolism and low feeding rates of snakes, their direct contact with contaminated soil, and the high levels of environmental contamination in Fukushima. We also hypothesized snake behavior would lead to high variation in external dose rates recorded by OSL dosimeters on snakes and those estimated via ERICA.

METHODS

Study Area

Located on the eastern coast of Japan, the Fukushima Daiichi Nuclear Power plant (FDNPP) was damaged by a tsunami in March 2011 following the largest earthquake in Japanese history. Approximately 520 PBq of radioactive materials were released into the atmosphere, including 6.1-62.5 pBq of ^{137}Cs (Steinhauser et al. 2014, Strand et al. 2014). Due to the release of contaminants, almost 120,000 people were evacuated from areas surrounding the power plant (Ohnishi 2011).

Forested areas made up more than 75% of the evacuated land, with the remainder composed of <10% rice paddy fields, <10% other agricultural fields, and <5% urban areas (Steinhauser et al. 2014). Although radiation levels had decreased to safe levels and evacuation orders were lifted for much of the evacuated areas by 2017, a large portion of the landscape northwest of the reactor still contains sufficiently high radiation to prevent humans from returning (Fukushima Prefectural Government 2019). Deemed the "Difficult-to-return Zone" by the Japanese, we refer to this evacuated area as the Fukushima Exclusion Zone (FEZ) throughout this paper. Despite the elevated levels of radionuclides that persist within the FEZ and are accumulated at high rates by some species (Kubota et al. 2015, Tanoi et al. 2016, Fuma et al. 2017), many wildlife species are abundant and widely distributed throughout the contaminated region (Lyons et al. In Press).

Our study sites consisted of two sampling areas (high and low contaminant levels) in the Abukuma Highlands of Fukushima Prefecture, Japan. Snakes were sampled within the FEZ from 19.4 to 34.4 km northwest of the FDNPP. We also sampled snakes further northwest in regions that were never evacuated and contain near background levels of radiation ("outside FEZ") (Fig. 4.2). Two snakes were collected within 1 km of the outer FEZ boundary but were included as "outside FEZ". Capture locations of snakes outside the FEZ ranged from 42.5 to 58.6 km northwest of the FDNPP. The average temperature during the study period was approximately 22.7 °C (annual average: 13.9 °C), and the annual precipitation for the region was 1,092.5 mm in 2018 (Japan Meteorological Agency 2018). The terrain was hilly with numerous streams and rivers and an elevation range of 49.26 – 754.42 m (mean: 437.67 m) across the two sampling areas.

Sampling

We collected live and freshly road killed snakes by hand in May through August 2018 that we opportunistically encountered on roads while driving among field sites for an unrelated study. We captured three snakes we opportunistically encountered in areas other than roads (e.g., forest, near building). We also included one additional snake previously collected as roadkill in July 2017 and stored frozen until use in this study. Upon capture, we took a GPS location and quantified relative contamination at each capture location by measuring ambient dose rates at approximately 1-m above the ground using a handheld dose-rate meter (Hitachi ALOKA TSC-171). For snakes captured on the road surface, we took dose rate measurements over soil at the roadside. We bagged snakes in pillowcases and placed them in plastic bins during transfer to the Institute of Environmental Radioactivity (IER) at Fukushima University. We recorded sex and morphological measurements (tail length, total length, snout-vent length, mass) and housed them in glass tanks with shelter and water until they could be measured (live) for radioactivity, after which we returned snakes to their capture locations as soon as possible (1-3 days). We transported roadkill snakes from the field in a cooler and stored them frozen until measuring their radioactivity. Due to small size or damage inflicted by vehicles, we were unable to determine the sex of some snakes. The most commonly encountered snake species in the area were the Japanese rat snake (*Elaphe climacophora*) and the Japanese striped snake (*E. quadrivirgata*). Other species collected via roadkill were the yamakagashi or tiger keelback (*Rhabdophis tigrinus*) and Japanese burrowing rat snake, (*Euprepiophis conspicillata*). We also encountered hibakari or “one-day snake” (*Amphiesma vibakari*), white banded snake (*Dinodon* *orientale*), and the Japanese mamushi (*Gloydius blomhoffii*), but did not include them in this study due to poor specimen condition and/or low sample size.

To quantify the radiation dose free-ranging snakes are exposed to within the FEZ, we attached GPS/UHF transmitters (~4 g, Alle 60, Ecotone Telemetry, Poland) to a subset of *Elaphe* spp. larger than >80 cm snout-vent length (SVL) that were initially captured for whole-body radiocesium counts. Detailed methods are provided in Chapter 2, but in brief, we used super glue to secure each transmitter to a strip of duct tape wrapped around each snake, then glued optically stimulated luminescence (OSL) dosimeters wrapped in parafilm to the transmitter to record dose accumulation. In order to track and recapture snakes and OSL dosimeters at the end of the study, we also attached a VHF transmitter (~1 g, BD-2, Holohil Systems Ltd., Ontario, Canada) in the same manner. The combined extra weight was no more than 5% of the snake's mass, and we positioned the transmitters on the snake's back far enough along the body to avoid increasing its maximum height. We allowed snakes to acclimate to the transmitters overnight, and then released them at their capture location the following day. Whenever we recaptured a snake (See Chapter 2), we removed the OSL dosimeter and replaced it with a new one, leading to multiple dose measurements for some snakes.

Analyses

Radiocesium Activity Concentrations

We measured whole-body radiocesium activity concentrations of all snakes by placing them inside Marinelli beakers on top of a High Purity Germanium Detector (HPGE) and recording the amount of gamma rays emitted in counts per second (c/s). Radiocesium concentrations in the gut content were likely small compared to the total body burden, and thus we did not expect gut contents to overly influence the results (Staton et al. 1974). To determine the efficiency of the whole-body counting system, we constructed snake size-specific gamma counting efficiency curves (Bq per c/s) using software associated with the analytical systems. These were confirmed by obtaining radiocesium burdens in the dissected and ground tissues of roadkill snakes of varying masses and equating this to the live whole-body counts estimated from the analytical software. We analyzed gamma-ray peaks of 604.6 keV for ^{134}Cs and 661.6 keV for ^{137}Cs. We ran each sample long enough to ensure measurement error was less than 10% for the total absorption peak of ^{137}Cs. We used linear regression with package lme4 in Program R (R Core Team 2017) to examine the effects of snake species, sex, SVL, and zone of capture (inside/outside FEZ) on whole-body radiocesium activity concentrations (^{134}Cs + ^{137}Cs). We ran an additive model with all the variables, and also tested for interactions between species and SVL, and species and sex. Due to small sample sizes of other species (Table 4.1), we only used *Elaphe* spp. in these analyses. To reduce variation due to differences in environmental contamination levels, we normalized the radiocesium activity concentrations for each snake to the ambient dose rate by dividing the activity concentration by the ambient dose measurement taken at its capture location. We also ran a regression with the ambient environmental dose rates and whole-body activity concentrations (both log-transformed to satisfy normality assumptions) and tested for correlation between by calculating the non-parametric Kendall's Tau correlation coefficient.

To quantify soil radiocesium activity concentrations, we collected three soil samples (ten cm deep soil core with five cm diameters) at randomly generated points within the 50% core area of each snake's home range (See Chapter 2), for a total of 21 soil samples. We measured ambient dose rates at each collection point at surface level and one-meter above the ground at each soil sampling location using a Hitachi TCS-172 NaI scintillation meter. We dried samples at 80 ºC and then homogenized them before measuring radiocesium following International Commission on Radiological Protection (ICRP) procedures (ICRP 2009b;a). We analyzed all soil samples for radiocesium activity concentrations using HPGE (GC3018, Canberra, Japan, Toyko).

Dose Rates

We estimated both internal and external dose rates to snakes captured in this study. We derived internal dose rate to snakes from measured whole-body radiocesium (^{134}Cs and ^{137}Cs) activity concentrations and a radionuclide-specific Dose Conversion Coefficient (DCC) using the ERICA tool (v. 1.3, updated May 2019). We estimated external dose rates to snakes in three different ways: 1) ERICA and the default concentration ratio (CR) for reptiles (0.574 Bq/kg), 2) ERICA and a Fukushima-specific CR derived from radiocesium activity concentrations measured from soil samples, and 3) dose accumulated by OSL dosimeters placed on snakes,. The CR is the activity concentration in the organism's whole body (Bq/kg fresh weight) divided by the activity concentration in the soil (Bq/kg dry weight). When animal tissue activity concentration data exist, but not soil activity concentration, ERICA uses the CR to back-calculate the soil activity concentration for each snake, which it then multiplies by the DCC to estimate external dose rate (µGy/h) received by the snakes.

ERICA creates the DCC separately for each snake based on inputted size parameters. We used the total length and mass measured for each snake, and estimated diameter based on a linear regression calculated from a set of captive and wild rat snakes with known measurements. Given that organism size has a minor impact on dose estimates relative to other sources of uncertainty, like the CR (Jaeschke et al. 2013, Charrasse et al. 2019), we didn't expect diameter estimations to overly bias our results. Within the ERICA model, we set the radiation source to infinite volume rather than a planar source, since radiocesium has begun to distribute through the soil layer in the years after the accident (Konoplev et al. 2018), and our soil samples detected radiocesium down to a soil depth of 10 cm. We calculated external dose for all snakes with the model's occupancy factor set for the snake residing 100% time "on soil", rather than partitioning a portion of the snakes' activities underground. Some snake species do indeed use underground burrows (Goris and Maeda 2004), but for the initial external dose calculations we opted to assume 100% above ground occupancy.

Following the same settings detailed above, we then estimated external dose based on soil samples collected in the home ranges of the snakes tracked with GPS and OSL dosimeters. For each tracked snake, we used the average soil activity concentration of the three samples collected in its range to calculate an individual-specific CR and external dose estimate. We averaged the CRs of the tracked snakes to create a Fukushima-specific CR to use in external dose estimation for all the other snakes in this study (for which we had no home-range specific soil activity data). We then compared the external doses estimated with our Fukushima-specific CR to those estimated using ERICA's default CR.

Although we initially calculated external dose using the 100% "on soil" occupancy factor, considering the ecology and behavior of an organism can significantly change the estimated exposure levels (Beaugelin-Seiller et al. 2018), so we used ERICA to quantify changes in estimated external dose rates under different occupancy scenarios informed by snake behavior. We ran a subset of snakes with 12 different percentages of time spent "in air" (as in a tree), "on soil", and "in soil" to reflect potential variation in individual behavior including arboreal, terrestrial, and underground habitat use. Snakes used for these analyses were the same snakes from which we tracked and recovered OSL dosimeters, and we used the Fukushima-specific CR for these tests. We ran snakes under the wildlife group "reptiles" with the specimen being "bird/flying insect" to allow for time spent "in air" to be adjusted. We calculated the percent change in estimated external dose from 100% “on soil” for each new occupancy scenario (e.g., 75% “on soil”, 25% “in air”).

OSL dosimeters integrated external dose the snake experienced over a known time period and we calculated dose rate (µGy/h) based on the number of hours the OSL dosimeter was attached to the snake. Although the dose recorded by the OSL dosimeters likely includes some contribution from radiocesium in the snake itself, we expected the internal contribution to be small due to 1) the cylindrical geometry and smaller size of a snake compared to that of larger mammals (Aramrun et al. 2019, Hinton et al. 2019), 2) the proximity of the OSL dosimeter to high levels of contamination in the surrounding environment, and 3) the placement of the OSL dosimeter on the outside surface of the GPS unit, which shielded the dosimeter from contamination internal to the snake (Fig. 4.1). We thus use dose obtained by the OSL dosimeter to approximate external dose. After log-transforming data, we ran linear regression models and tested for correlation with non-parametric Kendall’s Tau correlation coefficient for external dose rates and whole-body activity concentrations, as well as between external dose rates and ambient environmental dose rates.

RESULTS

We captured 55 snakes of four species (*Elaphe climacophora, E. quadrivirgata, Rhabdophis tigrinus, Euprepiophis conspicillata*), with 26 snakes from inside the FEZ and 29 snakes outside the FEZ (Table 4.1). Overall, we caught 27 live snakes and collected 28 roadkill snakes. Due to higher traffic, 66% of snakes from outside the FEZ were dead on the road compared to 35% of snakes from within the FEZ.

Average ambient dose rates for capture locations inside the zone were 2.6 ± 1.0 µSv/h (range: 1.4 – 5.6) and 0.2 ± 0.1 µSv/h (range: 0.01 – 0.5) for locations outside the FEZ. Whole-body radiocesium activity concentrations of all snakes were significantly correlated with the ambient dose measured at snake capture locations ($R^2 = 0.80$, *tau* = 0.60, $p < 0.0001$). After separately analyzing snakes captured inside and outside of the FEZ, the relationship remained significant for snakes captured outside of the FEZ ($R^2 = 0.25$, *tau* = 0.29 $p = 0.03$), but not inside the FEZ ($R^2 = 0.08$, *tau* = 0.10, $p = 0.49$) where snake radiocesium activity concentrations varied more widely (Table 4.2). The average whole-body radiocesium activity concentration (^{134}Cs + ^{137}Cs) of snakes from the FEZ (6,574 ± 5,944 Bq/kg [range: 1,105 – 24,726 Bq/kg]) was approximately 22 times higher than those from the less contaminated areas outside the FEZ (296 ± 567 Bq/kg [range: 16 – 2,995 Bq/kg], $p = 0.034$) (Table 4.3; Fig. 4.2). Mean radiocesium activity concentrations for *Elaphe quadrivirgata* were slightly but not significantly higher than *E. climacophora* (Fig.4.3). Neither species ($p = 0.84$), sex ($p = 0.34$), SVL ($p = 0.43$), nor the interactions of species x SVL ($p = 0.60$) or species x sex ($p = 0.43$) had a significant effect on normalized whole-body burdens of *Elaphe* spp. (Fig 4.4).

We deployed 16 OSL dosimeters on nine snakes within the FEZ (*Elaphe climacophora*, n = 8; *E. quadrivirgata*, n = 1). We removed and replaced the dosimeters on recaptured snakes, resulting in more than one dosimeter for some individuals. However, we were unable to recover five dosimeters because some snakes lost their GPS transmitters, resulting in 11 dosimeters from seven snakes (9 dosimeters from *Elaphe climacophora*, n = 6; 2 dosimeters from *E. quadrivirgata*, n = 1) for our analyses. The OSL dosimeters were deployed for an average of 11 ± 4 days (range: 5 – 20 days). The average dose rate from OSL dosimeters deployed on snakes was 2.2 ± 0.6 μGy/h (range: 1.3 – 3.2 μGy/h). Average OSL dose rates appear at first to agree remarkably well with the average ambient dose rate readings (2.6 ± 1.0 μSv/h); however, there was no correlation of OSL dose rates with ambient dose rates taken at snake capture locations

($R^2 = 0.07$, *tau* = 0.25, p = 0.31). Average OSL dose rates were positively but not significantly correlated with whole-body radiocesium activity concentrations ($R^2 = 0.17$, *tau* = 0.36, p = 0.13). Recovery of multiple OSL dosimeters from the same individual snake indicated that dose rates varied over time and location, although the maximum difference (0.7 µGy/h) was slight (Table 4.4).

The average soil activity concentration collected from the home ranges of tracked snakes was 2.38×10^4 Bq/kg (Table 4.4), and the average Fukushima-specific CR based on soil samples was 0.34 ± 0.28 (range: 0.10 – 0.95). Average external dose rates for all snakes calculated with the Fukushima-specific CR were within an order of magnitude but almost twice as high as the estimates produced with the default reptile CR in ERICA (Table 4.5). External dose, rather than internal, contributed most to the total dose for both estimates produced by the default CR (external = 62% of the total dose rate) and estimates using Fukushima-specific soil samples (external = 72% of the total dose rate) (Fig. 4.5).

The average total dose rate estimated with the Fukushima-specific CR for snakes from the FEZ was 2.8 µGy/h, compared to 0.2 µGy/h for those caught outside the FEZ. External dose rates of snakes were 2.8 ± 2.6 µGy/h (0.04 – 11.5 µGy/h) from the FEZ and 0.1 ± 0.2 µGy/h (range: 0.01 – 1.2 µGy/h) from outside the FEZ. External dose rates estimated with the Fukushima-specific CR were significantly correlated with the ambient environmental dose rates taken at snake capture locations ($R^2 = 0.78$, *tau* = 0.61, $p < 0.0001$). Similar to the relationship between ambient dose and radiocesium activity concentrations, the relationship remained significant for snakes caught outside the FEZ ($R^2 = 0.26$, *tau* = 0.33, p = 0.01) but not for snakes caught in more contaminated areas inside the FEZ ($R^2 = 0.21$, *tau* = 0.17, p = 0.22) (Table 4.2). For tracked snakes with OSL dosimeters, external dose rates calculated in ERICA and OSL dose rates were positively but not significantly correlated ($R^2 = 0.18$, *tau* = 0.43, p = 0.23). External doses estimated using soil samples within each tracked snake's home range were closer to observed OSL dose rates than estimates calculated with the default CR (Fig. 4.6). Internal dose rates for snakes from inside and outside the FEZ were 1.0 ± 0.9 µGy/h (0.2-3.7 µGy) and 0.4 ± 0.1 µGy/h (0.003 – 0.4 µGy/h), respectively.

Overall, 38% of snakes from the FEZ (n = 9) had greater than 5% chance of exceeding the suggested international screening dose limit of 10 µGy/h (Andersson et al. 2009) when calculated with 100% occupancy time on the soil surface. When modeling different occupancy scenarios in ERICA, manipulating the time spent in different habitats resulted in a change in the probability of exceeding the screening limit for all 7 snakes. The amount of time spent "in soil" had the largest influence on estimated dose rates, with the dose rate estimated from 100% time "in soil" more than 150% larger than the dose rate estimated from 100% time "on soil" (Table 4.6; Fig. 4.7). In contrast, selecting 100% time "in air" had only a 16% decrease in estimated dose rate. A roughly even split of 30% time spent in each habitat still resulted in a 30% increase in estimated dose compared to the 100% on soil scenario.

DISCUSSION

Here we provide a comprehensive analysis of radiocesium activity concentrations and dose rate estimates for snakes inhabiting a radiologically contaminated area in Fukushima, Japan. Radiocesium activity concentrations and total dose rates varied widely among snakes, likely due to differences in diet, behavior, and environmental contaminant levels within each animal's home range, but weren't significantly influenced by species, sex, or size. Our data present the first dose estimates recorded from dosimeters placed on free-ranging snakes, which indicated that external dose can vary temporally and spatially for a single individual depending on its behavior and habitat use. Although dose estimates produced with ERICA's default reptile CR and a Fukushima-specific CR were within an order of magnitude, selecting the default CR to estimate soil activity concentrations and the associated external dose underestimated dose received by the majority of the tracked snakes. External dose based on Fukushima-specific soil samples taken within the snakes' core home range areas generated external dose estimates more conservative and similar to those recorded by the OSL doses, with three times less variation than the default CR.

As we expected, external dose dominated total dose (contributing over 70% of the total), indicating that surrounding environmental contaminant levels had a larger contribution to the total dose than the radionuclides accumulated in snakes, possibly due to the lower bioavailability of radiocesium incorporated in Fukushima soils (Reinoso-Maset et al. 2020). Our modeling results illustrate that incorporating snake behavior and species-specific characteristics like arboreal climbing or burrowing tendencies in ERICA models has a considerable impact on estimated external dose rates and evaluation of potential risk for individuals inhabiting areas impacted by radionuclide contamination.

We found no support for radiocesium activity concentrations increasing with snake SVL in areas of both high and low contamination, despite the size range of snakes included in this study, suggesting factors other than snake size have a large influence on activity concentrations (Bagshaw and Brisbin Jr 1985, Takahara et al. 2015, Leaphart 2017). Although we could only test for species differences between *Elaphe climacophora* and *E. quadrivirgata* due to small sample sizes of other species, our results suggest these species exhibit similar radiocesium activity concentrations. Diet is an important factor in radiocesium accumulation (Murakami et al. 2014, Ishii et al. 2017, Nemoto et al. 2018), and because the two species often exhibit differences in diet – *E. climacophora* is an endotherm specialist (Mori 1996, Mori and Nagata 2016) while *E. quadrivirgata* often feeds on frogs (Mori et al. 1992, Hirai 2004, Mori and Nagata 2016) – we expected their radiocesium activity concentrations to differ. However, *E. quadrivirgata* is also a generalist predator, especially when frogs are limited (Ota 1986, Tanaka and Ota 2002, Hasegawa 2003, Mori and Vincent 2008). We did not quantify diet for either species, but dietary overlap may have reduced differences in radiocesium accumulation. Alternatively, snake diet and size may play a minor role in radiocesium accumulation compared to other factors like the distribution of radiocesium within an individual's home range, as the higher contribution of external dose to total dose in this study suggests. At the Savannah River Site, snakes with terrestrial diets had significantly lower radiocesium activity concentrations and higher variation in radiocesium loss than snakes with aquatic diets (Brisbin et al. 1974, Bagshaw and Brisbin Jr 1985), although this should be expected as radiocesium at the SRS occurs at higher levels in aquatic ecosystems due to the release of contaminants into reactor effluent streams (Jannik et al. 2013). In contrast to the SRS, radiocesium from the FDNPP was released via atmospheric deposition (Kato et al. 2018), resulting in a much wider distribution across the landscape such that variation in local contaminant levels may obscure differences in radiocesium accumulation due to snake diet.

Although radiocesium activity concentrations in Japanese rat snakes may be influenced by local environmental contaminant levels more than diet, seasonal variation in activity concentrations occurs in omnivores like wild boar (*Sus scrofa*) and black bear (*Ursus thibetanus*) due to shifts in diet (e.g., to fungi and underground food items that increase radiocesium ingestion) (Nemoto et al. 2018). It is possible snake diet varies seasonally (Hirai 2004) between prey with different contaminant levels, but as strict carnivores and as poikilotherms, radiocesium activity concentrations in snakes may be more stable throughout the year than those of mammals (Staton et al. 1974). The reduced metabolism and long biological half-life of radiocesium in snakes (average: 131 days) leads to little radiocesium loss of snakes during the winter (Staton et al. 1974), which suggests sampling activity concentrations of snakes during the spring and summer is sufficient to describe their annual radiocesium concentration.

Activity concentrations measured in organisms or the environment are typically used to estimate dose rates, but our use of OSL dosimeters on snakes provide a novel opportunity to compare observed dose rates with those estimated via the ERICA tool. External dose rates calculated in ERICA using the default CR and 100% time “on soil” underestimated the dose recorded by OSL dosimeters for 73% of the dosimeters (n = 8; Table 4.4). Even the dose rates calculated with ERICA’s default CR under the conservative 100% “in soil” occupancy scenario still underestimated 36% of the OSL dosimeters (n = 4). Our dose rate estimations using Fukushima-specific soil activity concentrations within snakes’ home ranges varied less and were more conservative compared to the default CR. This lends support to recent studies which suggest that not incorporating wildlife movement and space use causes underestimations of dose rates (Aramrun et al. 2019, Hinton et al. 2019).

The CR has a substantial influence on external dose rate estimates and—by extension—total dose rates, since the external dose contributed over half of the total dose of snakes in this study. The extensive natural variation in CRs across sites has caused some authors to recommend using CRs summarized from multiple data sources (i.e., ERICA’s default CR) for assessments rather than solely site-specific data (Sheppard 2005, Brown et al. 2013). However, ERICA’s default reptile CR is based on limited data from a handful of studies – with none from Fukushima – which greatly increases the uncertainty in dose estimates. The low bioavailability of radiocesium in Fukushima due to soil composition may explain why the Fukushima-specific CR was lower than the default CR (Takahashi et al. 2017, Reinoso-Maset et al. 2020). Measuring CRs across different sites is essential to understanding radionuclide transfer to reptiles, and our direct measurements of soil and organism activity concentrations in Fukushima represent a valuable contribution to this dataset (Sheppard 2005, Wood et al. 2010, Wood et al. 2012). CRs are not always good predictors of organism activity concentrations due to differences in site characteristics and the simplification of radionuclide transfer to organisms (Wood et al. 2013). This is especially true for organisms with large home ranges, because environmental contaminant levels are averaged over a greater spatial area (Anderson et al. 2019). The strong correlations between ambient dose at snake capture locations and the whole-body activity concentrations and external dose estimates in this study suggest environmental contaminant levels are better predictors of organism concentrations and dose for species with small rather than large home ranges. Significant correlations of ambient dose and/or soil activity concentrations with organism activity concentrations have also been documented in frogs, insects, and some bird species in Fukushima (Matsushima et al. 2015, Takahara et al. 2015, Ishii et al. 2017, Saito et al. 2019). However, the lack of correlation for snakes from inside the FEZ when analyzed separately from those outside the FEZ may indicate that a single ambient dose measurement at the capture location doesn't fully explain the variance in organism activity concentrations and external dose in more highly contaminated areas—even for species like snakes with small home ranges. Thus, CRs are still useful for estimating organism activity concentrations and external dose rates.

The variation in observed OSL dose rates likely reflect differences in individual snake behavior and habitat selection that may influence external dose – for example, some individuals resided extensively in abandoned buildings or in trees away from contaminated soil (See Chapter 2). One caveat was that our frequent relocation/recapture of tracked snakes, necessitated by short GPS battery life, may have influenced snake behavior and corresponding dose. Nonetheless, our data provide valuable information on dose rates to snakes living in contaminated environments deemed too radioactive for human residence. Having multiple OSL dosimeters from the same individual over different time periods allowed us to confirm that dose rates can vary for the same individual throughout time and space (see EEC16, EEC20 and EEQ8 in Figure 4.4). This variation due to individual behavior (in addition to relatively small sample sizes) may contribute to the lack of significant correlation between observed OSL dose and the external dose estimated in ERICA. The period of time over which we tracked snakes with OSL dosimeters was relatively short (~5 - 20 days), but it's reasonable to assume the variation in dose rates would increase if OSL dosimeters were attached longer as the snakes exhibit wider suites of behaviors and navigate through different parts of their home range.

Our ERICA modeling results suggest individual and species-specific behaviors can substantially influence observed radiocesium activity concentrations in snakes. For example, when external dose rates were calculated with 100% time on soil surface, 9.0% (n = 5) of sampled snakes had a greater than 5% probability of being over the international screening limit that projects possible risk to the population. This suggests that while some individuals in highly contaminated areas may be over the limit, it's doubtful that enough of the population is at a high enough risk to affect reproduction or population size. However, when considering the life history and habitat selection of snakes, it's possible the time spent overwintering underground or in burrows surrounded by contaminated soil may increase dose rates and thus risk (Tagami et al. 2018). Modeling external dose rates for snakes with even 30% time "in soil" resulted in ~30%

rise in external dose, with an increased probability of snakes in more highly contaminated areas exceeding the screening limit. In a more dramatic scenario, snakes modeled with 75% of the time spent “in soil” had an increase in external dose of ~115%. While this may not be a likely scenario for the *Elaphe* spp. evaluated in this study, there are other snake species in Fukushima that are fossorial and may receive higher doses of radiation due to increased time spent in soil. These results support the change in ERICA’s default reptile occupancy factor to 100% “in soil” for conservativism in estimating external dose (Brown et al. 2016a). Although we expected arboreal behavior to reduce radiation exposure through increased distance from the contaminated soil, the overall effect was slight (~16% decrease with at 100% time spent at the maximum height of 10 m) compared to the effect of spending time “in soil”. In other words, any beneficial reduction in dose from the time snakes spend in arboreal habitats is outweighed by (equal or less) time spent in the soil. Incorporating wildlife behavior and habitat use may potentially increase the accuracy of estimated external doses (Hinton et al. 2013, Stark et al. 2017), but if the most conservative estimate is desired, ERICA’s default 100% in soil occupancy is sufficient.

Seven years after the accident, the average total dose estimated for snakes in this study were below the generic predicted no-effect dose rate (PNEDR) of 10 µGy/h (a screening value thought to be protective of an estimated 85% of all plant, invertebrate, and vertebrates) (Garnier-Laplace et al. 2008, Andersson et al. 2009), and well below UNSCEAR’s estimate of significant impacts on terrestrial communities (100 µGy/h) (United Nations Scientific Committee on the Effects of Atomic Radiation 2008). Even considering the higher radiation doses shortly after accident due to the 2.06-year half-life of ^{134}Cs, the average radiocesium total dose would still have been below these thresholds (~6.7 µGy/h) – not considering dose from shorter-lived radionuclides. However, these broad screening limits are meant to protect the majority of *all* species including organism that aren't as radiosensitive as vertebrates (Garnier-Laplace et al. 2008, Andersson et al. 2009). As a result, not all higher trophic level species may be adequately protected by the generic 10 μGy/h (Garnier-Laplace et al. 2008, Andersson et al. 2009). The estimated vertebrate specific PNEDR (2 μGy/h) is lower than the average total dose rate observed in this study, and although based on limited data these dose rates are unlikely to have population or ecosystem-level effects (Garnier-Laplace et al. 2008, Andersson et al. 2009). Accounting for soil activity concentrations by using the Fukushima-specific CR increased the maximum total dose estimates for individuals in our study, and dose rates for snakes in more contaminated areas in proximity to the reactor are likely to exceed even 10 μGy/h, especially closer in time to the accident. Given their long-life span, some individual snakes may have experienced dose rates high enough to have some effect after the accident, but there remains scarce information on benchmark dose rates and dose effects specific to reptiles (Real and Garnier-Laplace 2019).

Similarly, our results address the lack of information on radiocesium concentrations in snakes in the FEZ and the surrounding region. We illustrate that snakes can accumulate relatively high radiocesium concentrations, depending on local environmental contamination. We also note that several individuals captured outside the FEZ had higher than expected radiocesium concentrations. The levels of 14 snakes exceeded the limit for consumption (100 Bq/kg) in Japan, even up to 15 - 24 km from the FEZ. One individual captured 15.6 km from the FEZ had a radiocesium activity concentration of 1,137 Bq/kg. Although wildlife can roam freely across the border of the FEZ, snakes have relatively limited home ranges compared to other species and are unlikely to travel distances of several kilometers (See Chapter 2). Thus, snakes may act as bioindicators, as environmental contaminant levels affect activity concentrations to a higher degree than snake diet or size. Because the contribution of external dose dwarfs that of internal dose, accounting for snake behavior and local environmental contaminant levels will reduce uncertainty in dose estimates and result in more accurate risk assessments.

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Table 4.1: Total number and species of snakes collected inside and outside of the Fukushima Exclusion Zone (FEZ) from May to August 2018 Fukushima, Japan. The numbers in the table are the total count of individual snakes collected, with the number of specimens collected dead on the road for each group in parentheses.

Species	Inside FEZ	Outside FEZ	Total
Japanese rat snake *Elaphe climacophora*	18 (3)	15 (9)	33 (12)
Japanese striped snake *Elaphe quadrivirgata*	6 (4)	9 (6)	15 (10)
Tiger keelback *Rhabdophis tigrinus*	0 (0)	4 (4)	5 (5)
Burrowing rat snake *Euprepiophis conspicillata*	1 (1)	1 (1)	2 (2)
Total	**29 (8)**	**26 (22)**	**55 (30)**

Table 4.2: Relationship between ambient dose rates, whole-body radiocesium activity concentrations (RAC), and estimated external dose rates for snakes collected in and around the Fukushima Exclusion Zone (FEZ) in June 2017 to August 2018. The linear regression equations and R^2 values are given for 1) ambient dose rates taken at snake capture locations and whole-body radiocesium activity concentrations and 2) ambient dose rates and external dose rates estimated in ERICA (Environment Risk from Ionising Contaminants Assessment and Management) using a Fukushima-specific concentration ratio. Regression equations and R^2 values were calculated for all snakes combined in addition to subsets of data based on snake capture location.

	All		Inside FEZ		Outside FEZ	
	Equation	R^2	Equation	R^2	Equation	R^2
Ambient dose and whole-body RAC	$y= -5 + 0.67x$	0.80	$y = 6.5 + 0.84x$	0.25	$y = 7.9 + 0.64x$	0.08
Ambient dose and estimated external dose	$y = -0.51 + 1.2x$	0.78	$y = -0.61 + 1.4x$	0.21	$y = -1.3 + 0.86x$	0.26

Table 4.3: Whole-body radiocesium activity concentrations and dose rates for 55 free-ranging snakes collected in Fukushima, Japan from July 2017 to August 2018. The dose rates were estimated in the ERICA (Environment Risk from Ionising Contaminants Assessment and Management) tool. Internal dose rates were calculated using the whole-body activity concentrations, and external dose rates were calculated using a Fukushima-specific concentration ratio using soil activity concentrations collected in the Fukushima Exclusion Zone.

ID	Zone	Species*	Sampling Date	Sex	Total length (cm)	Mass (g)	Activity concentration, Bq kg^{-1} FM			Internal dose rates µGy h^{-1}			External dose rates µGy h-^{1}			Total dose rates µGy h-^{1}
							^{134}Cs	^{137}Cs	Total	^{134}Cs	^{137}Cs	Total	^{134}Cs	^{137}Cs	Total	
EEQ1	E	Ela qua	22-May-2018	M	73.6	64	1,136	12,029	13,165	0.16	1.39	1.56	0.38	11.08	11.46	13.02
EEC1	E	Ela cli	25-May-2018	F	129	345	712	6,577	7,289	0.10	1.03	1.13	0.64	2.16	2.80	3.93
EEQ2	E	Ela qua	25-May-2018	F	60.7	34.3	673	6,115	6,788	0.09	0.95	1.04	0.22	5.53	5.75	6.79
CEQ3	C	Ela qua	27-May-2018	F	101.1	224.4	22	204	226	0.00	0.03	0.01	0.01	0.19	0.19	0.23
CEC2	C	Ela cli	29-May-2018	F	86.2	94.5	4	57	61	0.00	0.01	0.01	0.00	0.02	0.02	0.03
CEC3	C	Ela cli	29-May-2018	M	116	155.3	21	195	216	0.00	0.03	0.03	0.02	0.06	0.08	0.12
CEQ4	C	Ela qua	29-May-2018	F	81.7	90.2	11	83	94	0.00	0.01	0.01	0.01	0.03	0.04	0.05
CEQ5	C	Ela qua	2-Jun-2018	M	105.3	158.9	9	86	95	0.00	0.01	0.01	0.01	0.03	0.04	0.05
CRT4	C	Rha tig	2-Jun-2018	NA	21.6	2.76	111	1,026	1,137	0.01	0.13	0.14	0.10	0.35	0.45	0.59
CEC4	C	Ela cli	3-Jun-2018	M	113.6	181.6	27	249	276	0.00	0.04	0.04	0.02	0.08	0.11	0.15
CEC5	C	Ela cli	3-Jun-2018	F	85.9	123.3	17	157	174	0.00	0.02	0.03	0.02	0.05	0.07	0.09
CEQ6	C	Ela qua	3-Jun-2018	M	76.4	55.2	12	130	142	0.00	0.02	0.02	0.01	0.01	0.02	0.04
EEC6	E	Ela cli	4-Jun-2018	F	120.8	230.5	471	4,130	4,601	0.06	0.63	0.70	0.43	1.36	1.79	2.49
EEC7	E	Ela cli	4-Jun-2018	M	143.3	415.7	387	3,758	4,145	0.05	0.58	0.63	0.35	1.23	1.58	2.21
CEC8	C	Ela cli	5-Jun-2018	M	114.9	174.9	3	26	29	0.00	0.00	0.00	0.00	0.01	0.01	0.02
CEC9	C	Ela cli	5-Jun-2018	M	120.2	227.6	2	24	26	0.00	0.00	0.00	0.00	0.01	0.01	0.01
EEQ14	C	Ela qua	5-Jun-2018	NA	33.4	5.56	41	75	116	0.00	0.01	0.01	0.04	0.03	0.06	0.08
CEC10	C	Ela cli	5-Jun-2018	F	113.7	218.72	56	509	565	0.01	0.08	0.09	0.05	0.17	0.22	0.30
CRT6	C	Rha tig	5-Jun-2018	NA	24.7	4.06	13	87	100	0.00	0.01	0.01	0.01	0.03	0.04	0.05
CEQ7	C	Ela qua	5-Jun-2018	F	62.5	42.1	3	24	27	0.00	0.00	0.00	0.00	0.01	0.01	0.01
CEC11	C	Ela cli	6-Jun-2018	F	133.3	327.2	11	105	116	0.00	0.02	0.02	0.01	0.03	0.04	0.06
EEC12	E	Ela cli	8-Jun-2018	F	117.7	206.6	271	2,789	3,060	0.04	0.43	0.46	0.25	0.92	1.17	1.63
EEC13	E	Ela cli	8-Jun-2018	F	92.2	82.5	478	4,256	4,734	0.06	0.63	0.68	0.44	1.42	1.86	2.54
CEC14	C	Ela cli	17-Jun-2018	M	47.6	16.66	2	14	16	0.00	0.00	0.00	0.00	0.01	0.01	0.02
EEC15	E	Ela cli	23-Jun-2018	M	101.6	124.5	299	2,792	3,091	0.04	0.42	0.45	0.27	0.93	1.20	1.65
EEQ8	E	Ela qua	25-Jun-2018	M	101.9	154.68	734	7,114	7,848	0.09	1.07	1.17	0.57	2.96	3.53	4.69
CRT8	C	Rha tig	26-Jun-2018	NA	46.6	13.53	5	35	40	0.00	0.00	0.01	0.00	0.01	0.02	0.02

EEC16	E	Ela cli	27-Jun-2018	M	149.6	444.5	336	3,218	3,554	0.05	0.51	0.56	0.39	2.17	2.56	3.11
EEC17	E	Ela cli	27-Jun-2018	NA	66	49.78	565	4,998	5,563	0.06	0.72	0.78	0.52	1.67	2.19	2.97
CEC18	C	Ela cli	28-Jun-2018	F	108.3	206.5	17	185	202	0.00	0.03	0.03	0.02	0.06	0.08	0.11
EEC19	E	Ela cli	30-Jun-2018	F	115.6	247.1	860	8,327	9,187	0.11	1.28	1.40	0.78	2.75	3.53	4.93
EEC20	E	Ela cli	30-Jun-2018	F	124.7	298.5	192	1,970	2,162	0.03	0.31	0.33	0.41	2.18	2.59	2.92
EEQ9	E	Ela qua	2-Jul-2018	M	108.2	166.6	2,442	22,284	24,726	0.31	3.37	3.68	2.23	7.38	9.61	13.28
CEC21	C	Ela cli	3-Jul-2018	M	91.6	109.68	25	224	249	0.00	0.03	0.04	0.02	0.07	0.10	0.13
CEC22	C	Ela cli	5-Jul-2018	F	91.9	104.5	6	55	61	0.00	0.01	0.01	0.01	0.02	0.02	0.03
CEQ10	C	Ela qua	5-Jul-2018	F	39.9	11.73	19	164	183	0.00	0.02	0.02	0.02	0.02	0.04	0.06
CEC23	C	Ela cli	5-Jul-2018	F	106.7	204.5	34	304	338	0.00	0.05	0.05	0.03	0.10	0.13	0.18
CEC24	C	Ela cli	7-Jul-2018	NA	117.1	207.76	23	218	241	0.00	0.03	0.04	0.02	0.07	0.09	0.13
EEQ11	E	Ela qua	8-Jul-2018	NA	31.2	5.3	188	2011	2,199	0.02	0.26	0.28	0.17	0.67	0.85	1.13
CEQ11	C	Ela qua	10-Jul-2018	M	93.9	126.2	7	68	75	0.00	0.01	0.01	0.01	0.02	0.03	0.04
EEC25	E	Ela cli	11-Jul-2018	F	107.8	180.5	461	5,420	5,881	0.06	0.82	0.88	0.38	2.03	2.40	3.28
EEC26	E	Ela cli	11-Jul-2018	F	157	538.5	548	5,384	5,932	0.08	0.86	0.94	0.44	2.36	2.80	3.74
CRT9	E	Rha tig	11-Jul-2018	NA	79.6	86.6	290	2,938	3,228	0.03	0.43	0.47	0.27	0.98	1.24	1.71
CEQ12	C	Ela qua	12-Jul-2018	NA	56	17.5	4	34	38	0.00	0.00	0.00	0.00	0.01	0.02	0.02
EEC28	E	Ela cli	13-Jul-2018	F	141.1	548.5	908	8,510	9,418	0.13	1.37	1.50	0.58	3.06	3.64	5.14
EEQ13	E	Ela qua	14-Jul-2018	F	90.6	101.74	777	7,258	8,035	0.09	1.07	1.17	0.71	2.41	3.12	4.29
EEC29	E	Ela cli	14-Jul-2018	F	74.8	57.42	168	1,297	1,465	0.02	0.19	0.21	0.15	0.43	0.59	0.79
CRT11	C	Rha tig	15-Jul-2018	NA	60.2	30.18	268	2,727	2,995	0.03	0.38	0.41	0.25	0.92	1.16	1.57
Ebur1	E	Eup con	15-Jul-2018	M	81	109.09	99	1,006	1,105	0.01	0.15	0.16	0.01	0.03	0.04	0.20
CEC30	C	Ela cli	16-Jul-2018	F	110.9	158.04	17	147	164	0.00	0.02	0.02	0.02	0.05	0.06	0.09
Cbur2	C	Eup con	16-Jul-2018	NA	83	75.29	49	537	586	0.01	0.08	0.08	0.05	0.18	0.22	0.31
EEC31	E	Ela cli	20-Jul-2018	F	126.1	276.5	2,307	21,598	23,905	0.31	3.35	3.66	0.50	2.66	3.16	6.82
EEC32	E	Ela cli	1-Aug-2018	F	122	250.5	434	4,246	4,680	0.06	0.65	0.71	0.39	1.40	1.79	2.51
EEC33	E	Ela cli	1-Aug-2018	F	136.1	472.5	181	1,788	1,969	0.03	0.29	0.31	0.16	0.58	0.75	1.06
EEC34	E	Ela cli	20-Jul-2017	M	131.2	348.6	279	2,914	3,193	0.04	0.46	0.50	0.25	0.96	1.21	1.70

*Ela qua = *Elaphe quadrivirgata*; Ela cli = *Elaphe Climacophora*; Rha tig = *Rhabdophis tigrinus*; Eup con = *Euprepiophis conspicillata*

Table 4.4: Radiocesium (^{134}Cs + ^{137}Cs) activity concentrations and dose rates of seven rat snakes (*Elaphe* spp.) tracked in the Fukushima Exclusion Zone (FEZ) with GPS transmitters during summer 2018. External dose rates quantified from optically-stimulated luminescence (OSL) dosimeters placed on tracked snakes are compared to external dose rates calculated in the ERICA (Environment Risk from Ionising Contaminants Assessment and Management) tool using 1) the default reptile concentration ratio and 2) Fukushima-specific soil activity concentrations sampled from within each individual's 50% home range. Radiocesium activity concentrations from the whole-body snake and soil samples are displayed along with the average ambient environmental dose rate taken at 1 m above ground at soil sampling locations.

Snake ID	**Radiocesium activity concentration**		**Ambient environmental dose rate (μSvh^{-1})**	**OSL dose rate (μGyh^{-1})**		**OSL average dose rate (μGyh^{-1})**	**ERICA external dose rate (μGyh^{-1})**	
	Snake (Bq kg^{-1} FW)	**Soil (Bq kg^{-1} DW)**		**1**	**2**		**Default**	**Fukushima-specific**
EEC16	3.55 E+03	2.07 E+04	2.77	2.44	2.30	2.37	0.80	2.56
EEC20	2.16 E+03	2.08 E+04	2.23	1.59	2.14	1.86	0.49	2.59
EEC25	5.88 E+03	1.92 E+04	2.67	-	1.27	1.27	1.32	2.40
EEC26	5.93 E+03	2.27 E+04	2.31	2.31	3.05	2.68	1.33	2.80
EEC28	9.42 E+03	2.95 E+04	2.92	2.50	-	2.50	2.12	3.64
EEC31	2.39 E+04	2.53 E+04	3.74	3.23	-	3.23	5.47	3.16
EEQ8	7.85 E+03	2.80 E+04	3.39	2.13	1.68	1.90	1.80	3.53

Table 4.5: Mean and standard deviation (SD) for the total dose and external dose estimates of 55 snakes captured inside and outside the Fukushima Exclusion Zone (FEZ) from May to August 2018. Dose rates were estimated in ERICA (Environment Risk from Ionising Contaminants Assessment and Management) with the default reptile concentration ratio (CR) and average Fukushima-specific CR informed by soil activity concentrations.

		Dose rates (μGyh^{-1})			
	n	Fukushima-specific CR		Default CR	
		Mean ± SD	**Range**	**Mean ± SD**	**Range**
Inside FEZ	**26**				
Total dose		3.79 ± 3.23	0.20 - 13.28	2.59 ± 2.40	0.41 - 9.13
External dose		2.82 ± 2.59	0.04 - 11.46	1.61 ± 1.62	0.25 - 6.80
Outside FEZ	**26**				
Total dose		0.16 ± 0.30	0.01 - 1.57	0.11 ± 0.21	0.01 - 1.10
External dose		0.12 ± 0.22	0.01 - 1.16	0.07 ± 0.13	0.003 - 0.69
Total	**55**				
Total dose		1.88 ± 2.87	0.01 - 13.28	1.28 ± 2.06	0.01 - 9.13
External dose		1.39 ± 2.23	0.01 - 11.46	0.80 ± 1.35	0.004 - 6.80

Table 4.6: Modeling results using the ERICA (Environment Risk from Ionising Contaminants Assessment and Management) tool to estimate radiation dose in snakes in Fukushima, Japan, illustrating the average percent change in estimated external dose rate under various behavioral scenarios relative to an estimate of 100% of time spent on soil.

Behavioral Scenario	**"In Air"**	**Time (%)** **"On Soil"**	**"In Soil"**	**Average Percent Change (%)**
Arboreal	100	0	0	-15.9
Arboreal, terrestrial	75	25	0	-11.9
Arboreal, terrestrial	50	50	0	-7.9
Arboreal, terrestrial	25	75	0	-4.0
Terrestrial	0	100	0	0.0
Terrestrial, Fossorial	0	75	25	49.1
Terrestrial, Fossorial	0	50	50	76.8
Terrestrial, Fossorial	0	25	75	115.1
Fossorial	0	0	100	153.5
Arboreal, Terrestrial, Fossorial	20	20	60	79.0
Arboreal, Terrestrial, Fossorial	30	30	30	31.3
Arboreal, Terrestrial, Fossorial	45	45	10	8.2

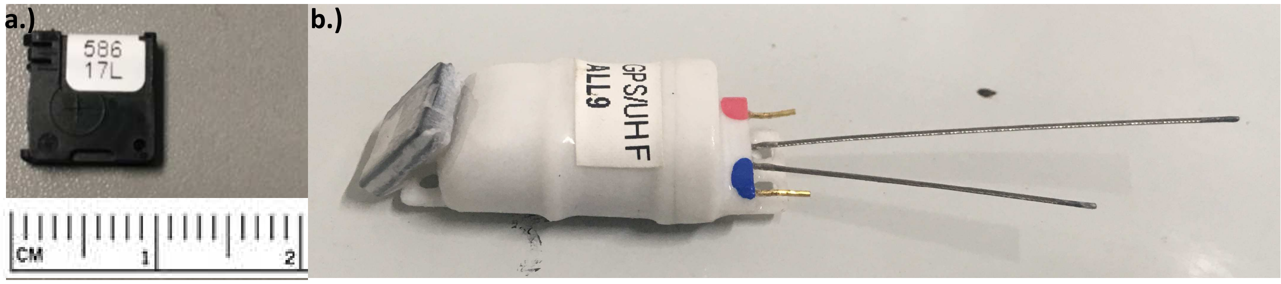

Figure 4.1: Example of a.) optically-stimulated luminescence (OSL) dosimeter and b.) OSL dosimeter attached to GPS/UHF unit used to measure external radiation dose to free-ranging rat snakes (*Elaphe* spp.) in the Fukushima Exclusion Zone in Japan.

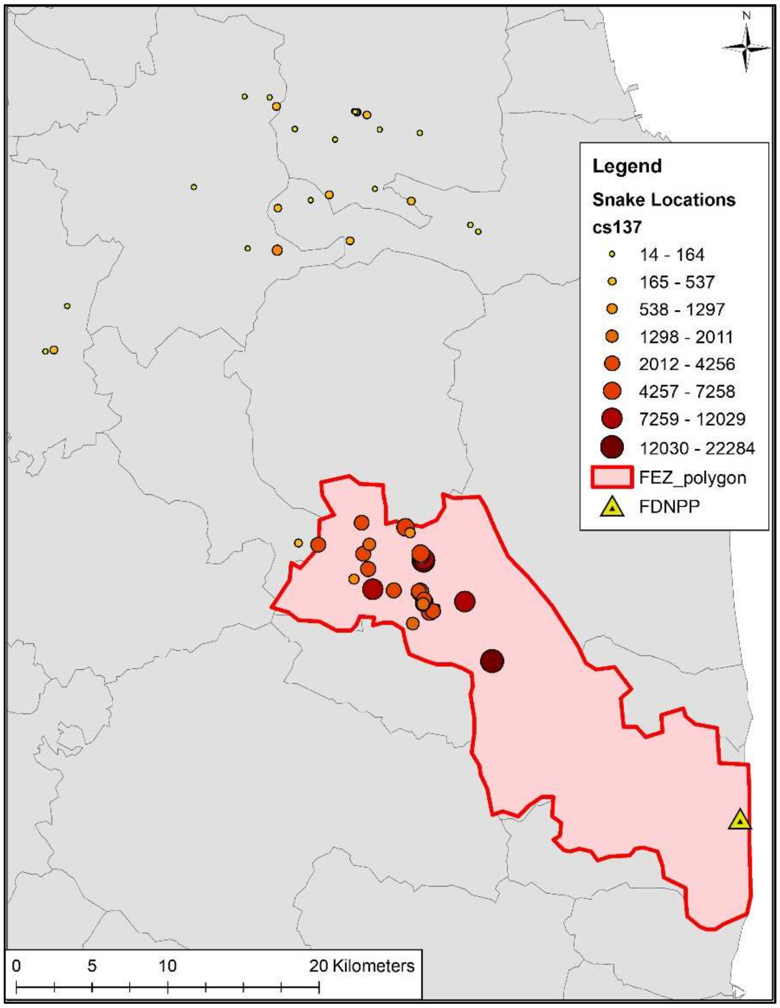

Figure 4.2: Map of capture locations for all snakes in relation to the Fukushima Exclusion Zone (FEZ; red shaded area) and the Fukushima Daiichi Nuclear Power plant (yellow triangle). Snake locations are represented by dots whose sizes are scaled to represent whole-body ^{137}Cs activity concentrations (Bq/kg FW).

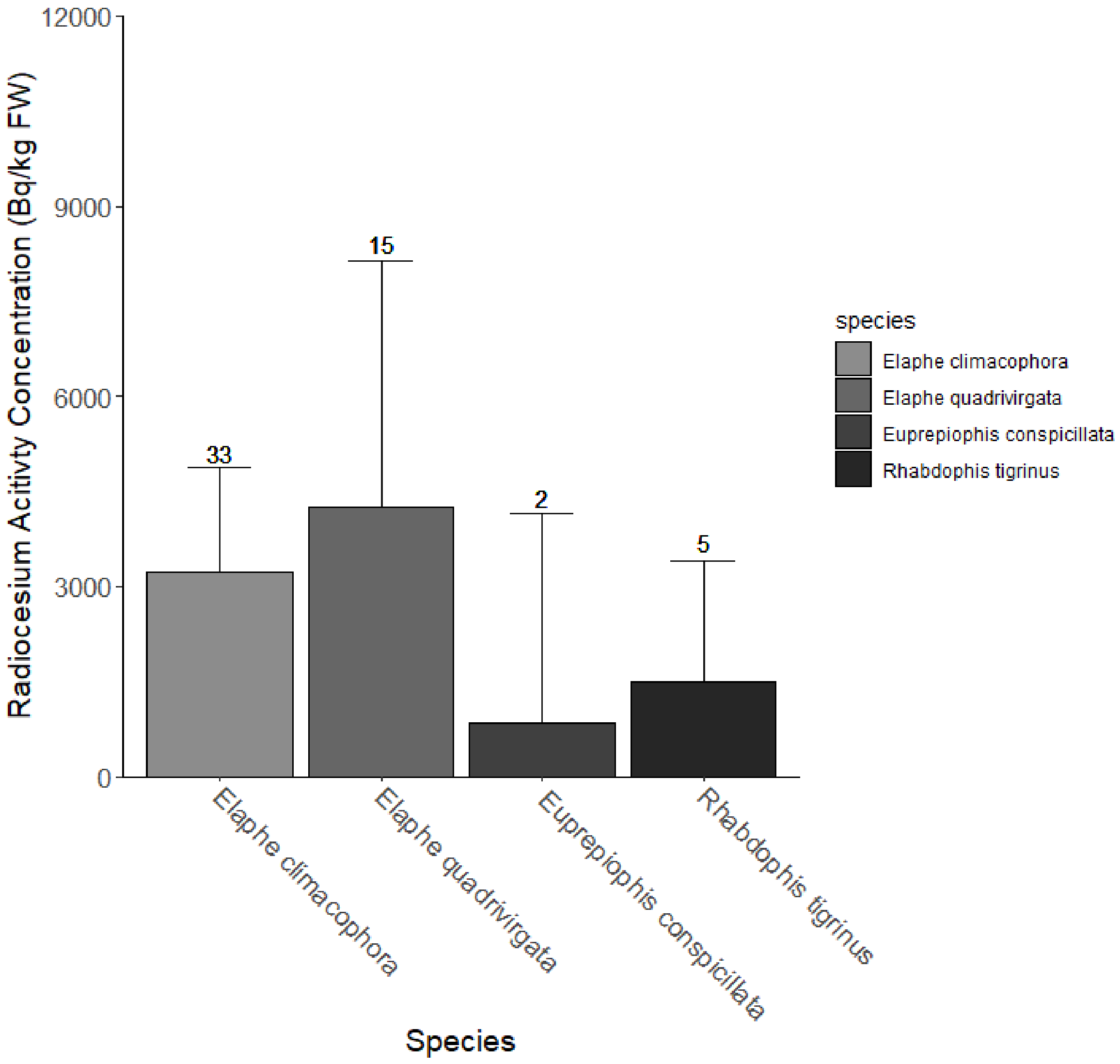

Figure 4.3: Mean whole-body radiocesium (^{134}Cs + ^{137}Cs) activity concentrations (Bq/kg FW) of snake species (*Elaphe climacophora, E. quadrivirgata, Euprepiophis conspicillata, Rhabdophis tigrinus*) captured in the Fukushima Exclusion Zone (FEZ) and surrounding area. Error bars represent confidence intervals with sample size specified for each species.

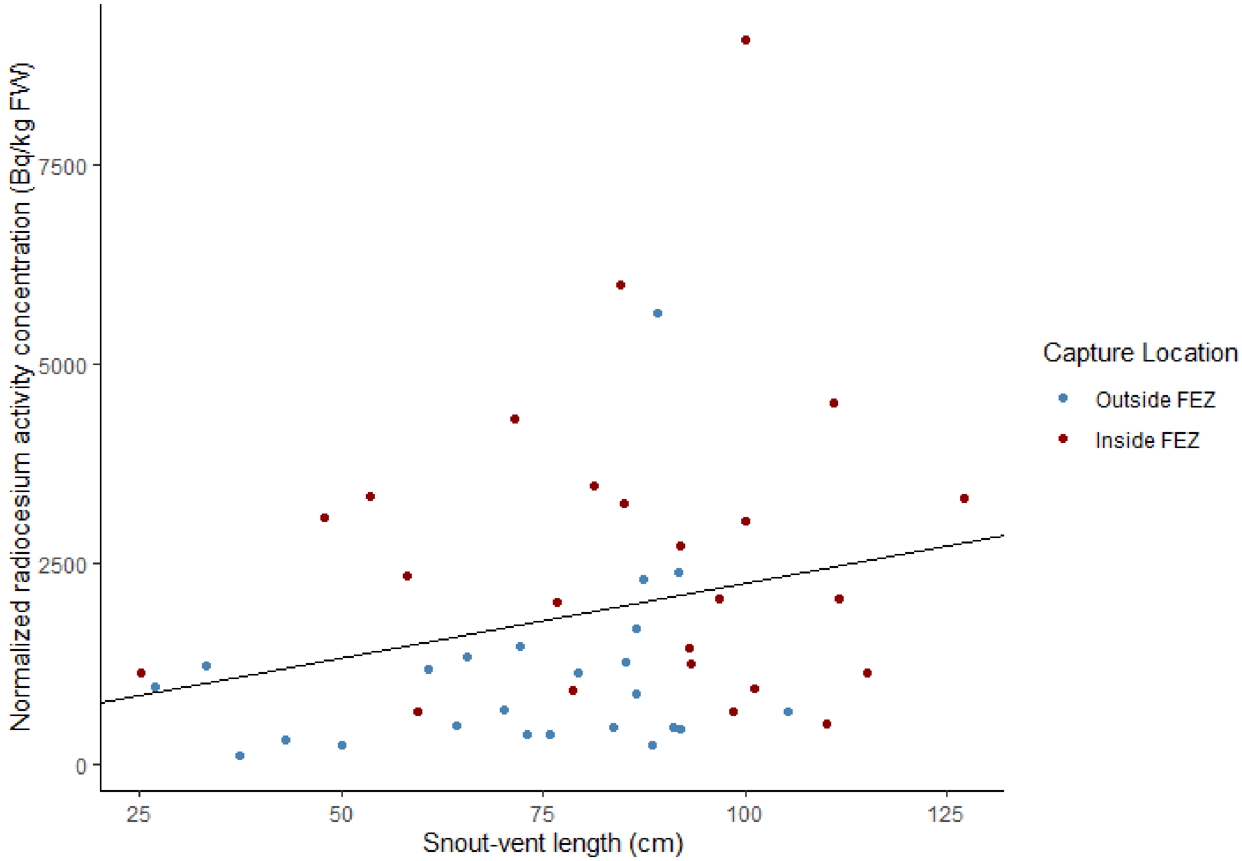

Figure 4.4: Normalized radiocesium activity concentrations by snout-vent length (SVL) for all rat snakes (*Elaphe* spp.) captured inside and outside the Fukushima Exclusion Zone (FEZ) from July 2017 to August 2018. Values were normalized by dividing radiocesium activity concentrations for each snake by the ambient dose rate recorded at its capture location.

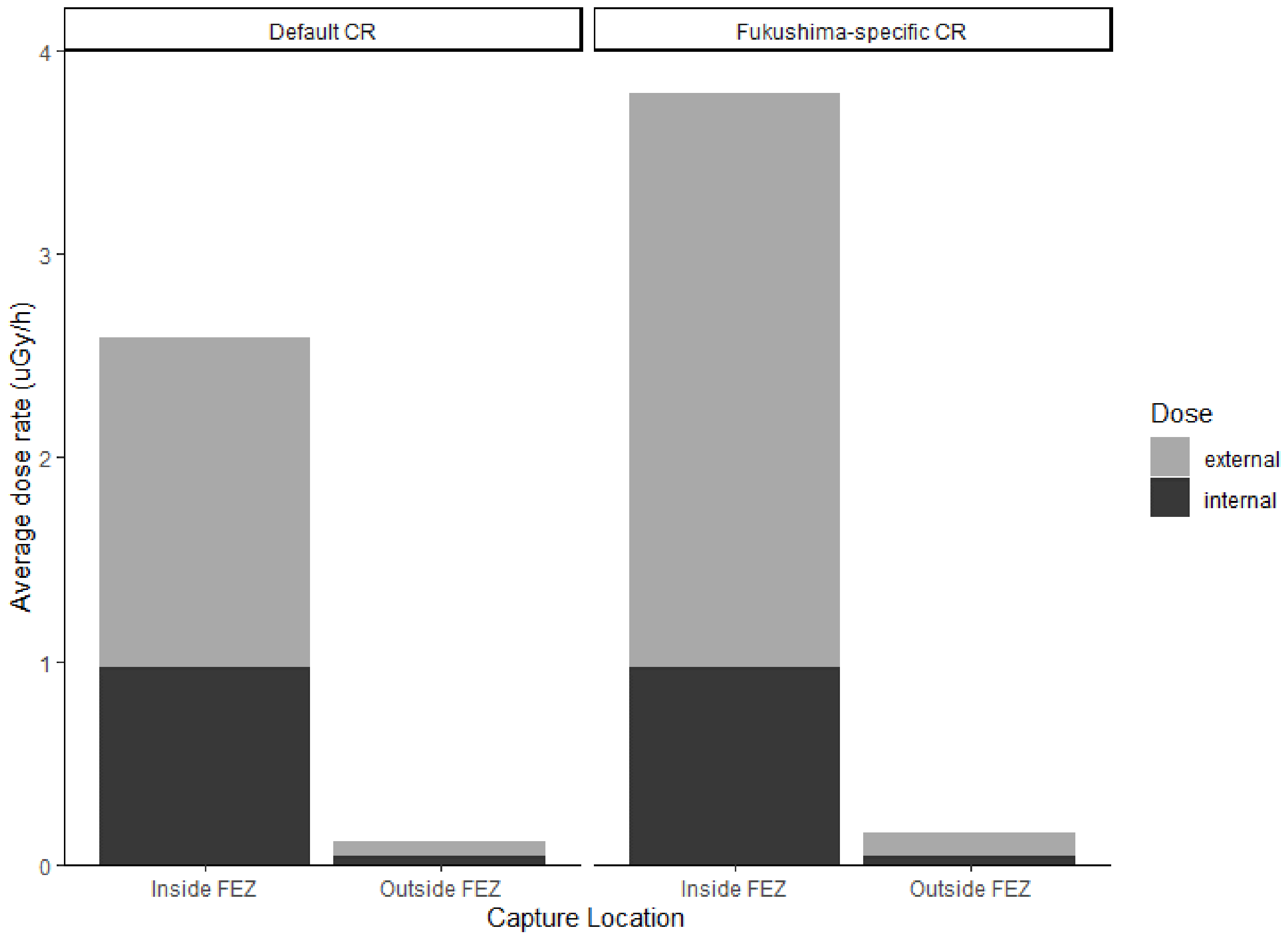

Figure 4.5: Average internal and external dose rates (µGy/h) estimated via the ERICA (Environment Risk from Ionising Contaminants Assessment and Management) tool for snakes caught inside and outside the Fukushima Exclusion Zone (FEZ). Dose rates were estimated with the 1) default reptile concentration ratio and 2) Fukushima-specific concentration ratio informed by soil activity concentrations.

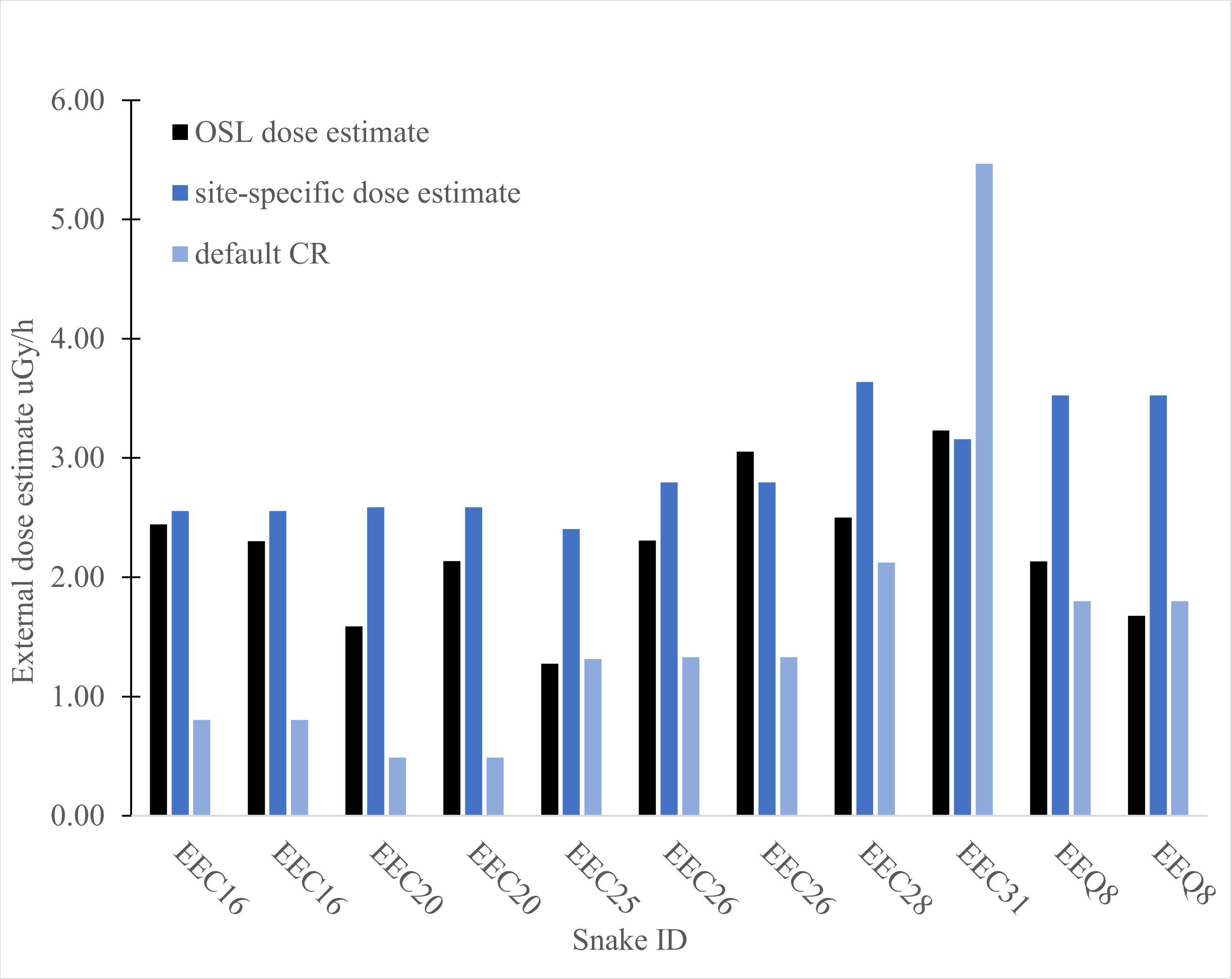

Figure 4.6: External dose rates (µGy/h) of rat snakes (*Elaphe* spp.) tracked in the Fukushima Exclusion Zone (FEZ) with GPS and optically-stimulated luminescence (OSL) dosimeters during summer 2018. This graph displays external dose recorded by 11 OSL dosimeters on 7 individual snakes and compares them to external dose estimates derived in the ERICA (Environment Risk from Ionising Contaminants Assessment and Management) tool using two methods: 1) the default reptile concentration ratio (0.57) used to derive soil radioactivity concentrations and 2) Fukushima-specific soil activity concentrations sampled from within each individual snake's 50% home range. For individuals with more than one OSL dosimeter, dose from both dosimeters are displayed, indicating how snake behavior can influence dose over time and space.

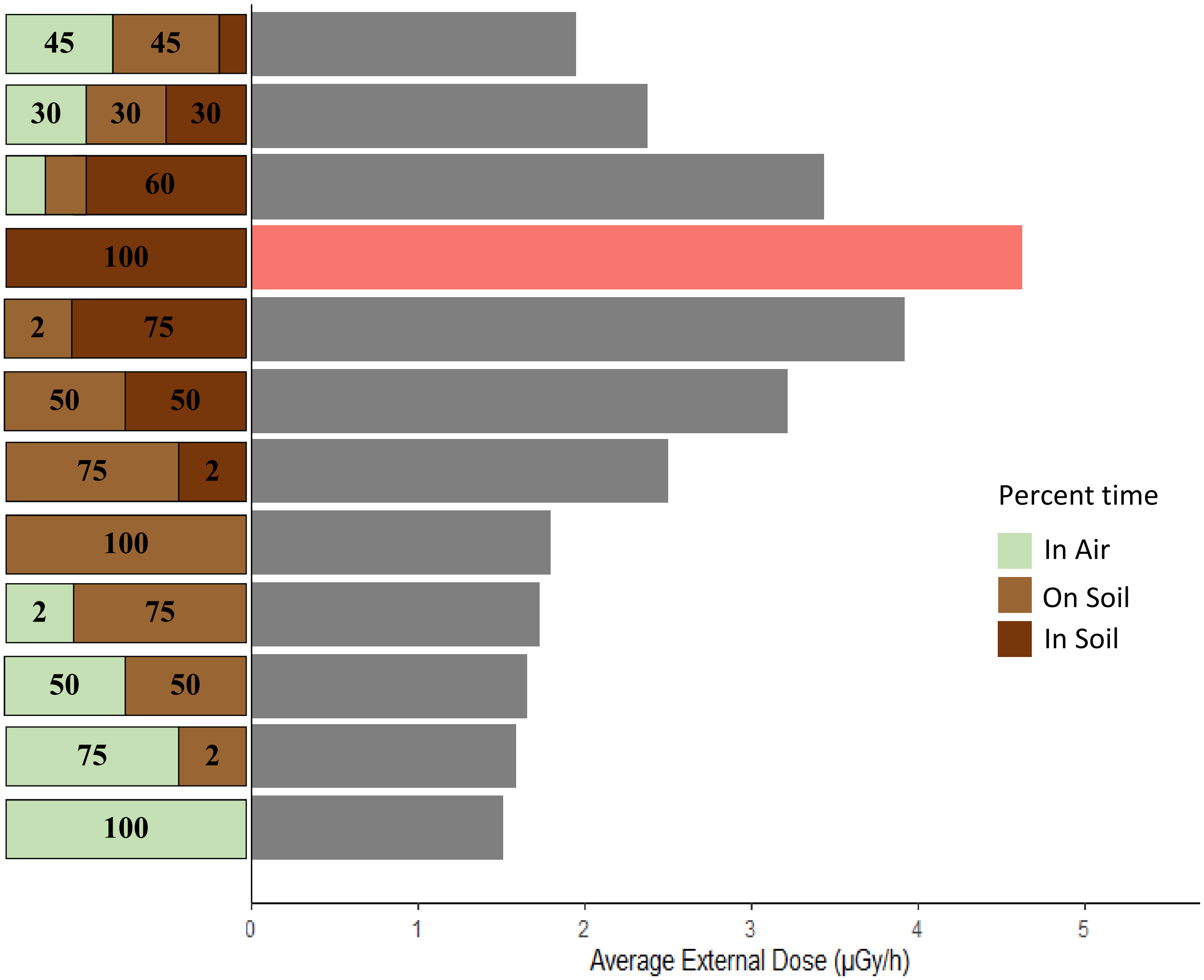

Figure 4.7: External dose rate (µGy/h) to snakes estimated using the ERICA (Environment Risk from Ionising Contaminants Assessment and Management) tool under different behavioral scenarios. Bars on the left represent varying percentages of time (out of 100%) spent in different habitats (in air, on soil, in soil) and bars on the right represent the corresponding external dose estimate. For reference, the red bar is ERICA's default occupancy for reptiles, 100% in soil.

CHAPTER 5

CONCLUSIONS

The Fukushima Daiichi Nuclear Power Plant accident in 2011 was one of the largest accidental releases of radiological contamination in human history, second only to the Chernobyl accident. Despite the push for research to determine the effects of chronic radiation exposure on biota, many of the ecological ramifications of these nuclear accidents remain unknown. For example, our ability to accurately estimate radiation dose and thus assess risk to wildlife is hindered by numerous uncertainties, which result from variation in the distribution and behavior of both wildlife and radionuclides in contaminated systems. Complicating our understanding of these ecological ramifications is that large nuclear disasters also impact ecosystems in ways other than radionuclide contamination—such as the creation of exclusion zones and mass shifts in human activity on the landscape. My thesis provides novel insight into the repercussions of the 2011 Fukushima Daiichi accident by providing the most extensive data to date on scavenging dynamics as well as the spatial ecology and radioecology of snakes within the FEZ.

In Chapter 2, I broadly examined the composition and efficiency of the vertebrate scavenger community in the FEZ compared to nearby areas where human activity was unaffected by the accident, which has implications for the stability of the ecosystem and its services. My results indicated that despite the presence of radiological contamination, vertebrate scavengers inside the FEZ were equally as diverse and efficient at assimilating carrion as in the surrounding landscape. I documented more than 20 wildlife species, with over 70% of all carcasses scavenged by 13 vertebrate scavenger species. The majority of vertebrate scavengers in this study were mammals, although I also observed avian and reptilian species scavenging. Of particular note, by using time-lapse in addition to the camera's motion-sensor it allowed me to detect a greater diversity of species that likely are often missed in many scavenging studies, including extensive scavenging by mice and several instances of scavenging behavior by snakes. The scavenging rates observed in this study were fairly high for the warm season, but were within the range reported in the literature (Olson et al. 2012, Turner et al. 2017, Sugiura and Hayashi 2018, Schlichting et al. 2019). Of the variables evaluated in this study (carcass size, habitat, and human activity zone), carcass size was the most important predictor of scavenging dynamics. As I expected, rabbit carcasses were scavenged by more species and persisted longer than mouse carcasses, while the smaller size of mouse carcasses allowed them to decompose or be usurped by invertebrates faster. The high percentage of carcasses scavenged by invertebrates like carrion beetles suggests intense competition exists between invertebrates and vertebrate scavengers for carrion resources, and suggests functional redundancy of carcass removal services among scavenging communities (Beasley et al. 2015, Sugiura and Hayashi 2018).

Although carcass size had the most pronounced influence on scavenging dynamics, I did observe differences in scavenging rates for some species between evacuated and inhabited areas. Wild boar—which are over three times more abundant in the FEZ where human activity is limited (Lyons et al. In Press)—scavenged and removed substantially more carcasses in the FEZ, which corresponded with higher scavenging rates by foxes in the control area. Such species-specific differences between zones may have implications for nutrient distribution in the food web, particularly if boar populations continue to expand in the FEZ. Collectively, the results of this study suggest a highly diverse and efficient scavenger community exists in the FEZ, and contributes to the ecosystem's capacity to provide ecosystem services and withstand the disturbances caused by the 2011 accident (Wilson and Wolkovich 2011, Mori et al. 2013).

In Chapter 3, I used a combination of VHF and GPS transmitters to estimate home range size and habitat selection of nine Japanese rat snakes (*Elaphe climacophora* and *E. quadrivirgata*) within the FEZ. From these data I estimated short-term aLoCoH home ranges, which were relatively small (0.15-6.80 ha) and revealed snakes moved short distances (30-116 m daily). These results support the idea that snakes may be useful bioindicators of local environmental contamination levels due to their limited movement. Although rat snake habitat selection differed slightly across spatial scales, they consistently avoided evergreen forests while selecting areas close to streams. The short-term ranges of snakes included more areas in proximity to anthropogenic features like buildings and roads, as well as more grassland (i.e. rice paddy) than expected given the availability of these land cover types at the population scale. Snakes frequently spent time in trees and abandoned buildings, which may influence radiation dose by altering their exposure to radioactive contaminants in the soil. My results from this chapter provide valuable insight into snake movement rates, behavior, and habitat selection within a contaminated landscape, which can be incorporated into models to reduce uncertainties in radiation dose estimates. In particular, extensive variation in habitat use by snakes helps explain the considerable heterogeneity in radionuclide accumulation and exposure observed among individual snakes in Chapter 4.

Using the knowledge of snake movement behavior gained in Chapter 3, in Chapter 4 I quantified whole-body radiocesium activity concentrations and generated dose estimations for snakes in the FEZ. In this chapter, I present one of the most comprehensive radioecological studies of snakes to date. Average radiocesium levels in snakes from the FEZ (6,574 ± 5,944 bq/kg) were 22 times higher than those collected in the surrounding landscape (296 ± 567 bq/kg), although some snakes captured outside the FEZ had surprisingly high radiocesium levels. Whole-body radiocesium activity concentrations did not vary by species, sex, or snake size. Instead, radiocesium concentrations in the snakes were most substantially influenced by local environmental contaminant levels. To further elucidate the underlying factors influencing radiation dose rates in snakes, in this chapter I also quantified the actual dose absorbed by dosimeters placed on free-ranging snakes in the FEZ, which can vary spatially and temporally depending on individual behavior and habitat use. Observed dose rates from dosimeters on wildlife are scarce (Hinton et al. 2015, Aramrun et al. 2018), and prior to this study had not been evaluated for snakes, yet are invaluable for evaluating dose estimations produced in computer simulated dose rates (e.g., ERICA) commonly used for wildlife dose estimations. External dose estimates produced in ERICA using a Fukushima-specific CR calculated from soil samples taken within the home ranges of tracked snakes resulted in estimates that agreed with those recorded by the OSL dosimeters. Thus, incorporating local contaminant levels using a site-specific CR can lead to more precise dose estimations. In contrast, using ERICA's default reptile CR underestimated 73% of the external doses recorded by dosimeters on snakes tracked in Chapter 3, and resulted in much lower dose estimates for all snakes in this study. Producing accurate dose estimations is essential, as underestimation could lead to incorrect risk assessments. The CR is one of the largest sources of uncertainty in dose estimations, in part because the default reptile CR is based on limited data. Data from this study (which are the first on reptiles in Fukushima) will be an important contribution to ERICA's database and will help reduce the uncertainties in future dose estimations. Finally, our modeling results also illustrate that incorporating snake behavior and species-specific characteristics like arboreal climbing or burrowing tendencies in

ERICA models has a considerable impact on estimated external dose rates and thus the evaluation of potential risk to individuals inhabiting radiologically contaminated areas.

Collectively, my research adds to our understanding of the ecological impacts associated with the 2011 Fukushima Daiichi Nuclear Power Plant accident. The diverse scavenging community supports previous research showing thriving wildlife communities in areas of limited human activity, and indicates that some ecosystem services have not been negatively affected by the 2011 accident. The results of my third and fourth chapters contribute to our limited knowledge of snake movement and exposure to radiation in a radiologically contaminated landscape, and represent the most comprehensive radioecological data on snakes to date. However, further research is needed to develop specific benchmarks for reptiles, and to assess the potential health impacts of chronic radiation exposure to individuals.

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