

SPATIOTEMPORAL DRIVERS OF FISHER (*PEKANIA PENNANTI*) HEALTH AND  
DEMOGRAPHY IN NEW YORK STATE

by

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## ABSTRACT

S.A. Cunningham. Spatiotemporal Drivers of Fisher (*Pekania pennanti*) Health and Demography in New York State, 204 pages, 11 tables, 20 figures, 6 appendices, 2023. Ecological Society of America style guide used.

Life history strategies of wildlife, and the expected variation in particular demographic rates (e.g., survival and recruitment), are useful for investigating how a species might respond to global change. Fishers (*Pekania pennanti*) experienced near-extinction levels of habitat loss and overharvest by the early 1900s, but populations have rebounded in the northeastern United States in recent decades. Yet, across New York, an area with high human population densities, harvest data indicated potential variation in population trend and density. In this dissertation, I sought to explore spatial variation in demographic rates across northern New York, which consisted of a gradient of biotic and abiotic conditions. I used data from harvested fishers to investigate exposure to anticoagulant rodenticide (AR), and emerging threat to wildlife, and camera traps and collared fishers to estimate demographic rates. Across New York State, ARs were found in 83% of fishers, and the number of compounds fishers were exposed to varied significantly as the surrounding area increased in wildland-urban interface (WUI), beechnuts produced in the previous year, age, and sex. However, variation in probability of exposure relative to WUI and beechnut count was not consistent for individual AR compounds. We collared fishers within two focal areas (Tug Hill and Adirondack Park), with younger forests and more WUI further west (Tug Hill). Annual survival rates were higher in Adirondack Park than Tug Hill. Yet, harvest mortality was higher in Tug Hill, Adirondack Park fishers had greater non-harvest mortality. On average, kit survival was higher and less variable in Tug Hill, with both WUI and forest stand age explaining significant variation in kit survival. Home ranges were larger and more variable in Adirondack Park, but not significantly. Despite the potential risk of mortality from ARs, fisher survival and kit production appear to be higher in more developed areas presumably due to greater prey availability. Overall, this dissertation provides evidence that fisher populations in Tug Hill appear characteristic of high-productivity systems that can support high harvest rates, while fisher management in Adirondack Park may need to account for sub-optimal habitats, and the restrictions on habitat management within the boundaries of Adirondack Park.

Key Words: anticoagulant rodenticide, camera traps, demography, forest carnivore, harvest management, kit production, life history, prey availability, mast cycles, recruitment, stand age, survival, telemetry, wildland-urban interface

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## **CHAPTER 1: INTRODUCTION**

### **LIFE HISTORY THEORY AND VITAL RATE TRADEOFFS**

Species have evolved different life history strategies, i.e., tradeoffs among growth, survival and reproduction (Stearns 1983, 1992, Gaillard et al. 1989), that have been honed through natural selection to maximize lifetime fitness (Philippi and Seger 1989, Ricklefs and Wikelski 2002). We might catalogue life histories along a continuum from ‘fast’ to ‘slow’ (Gaillard et al. 2005), with ‘fast’ tempos corresponding to short generation times, quick development, and high reproduction rates, and ‘slow’ tempos involving longer generation times, slower development, and fewer total offspring (Bielby et al. 2007, Dobson and Oli 2007). Physiological limits to growth and metabolism constrain tempo in larger animals, with fast tempos being generally restricted to smaller animals (Brown and Sibly 2006, Sibly and Brown 2007). That said, some characteristics (e.g., late sexual maturity and few offspring per litter; Bielby et al. 2007) consistently occur together regardless of body size, while other combinations (e.g., late sexual maturity and short lifespan; (Gaillard et al. 1989) are not observed at all (Ricklefs 2000, Ricklefs and Wikelski 2002, Healy et al. 2019). While all species have some ability to adapt to changing environmental conditions, specific life histories will likely see greater extinction risks in the face of short-term landscape and climate change, such as slow tempos resulting in longer generation times (Purvis et al. 2000).

Location-specific conditions, such as predictability of the environment in terms of the constancy or regularity of resources across space and time, will cause spatial variation in life history strategies (Colwell 1974, Zammuto and Millar 1985, Reed et al. 2010, Riotte-Lambert and Matthiopoulos 2020), which provides a lens through which long-term changes may be

observed (i.e., space for time substitution). Although elevational and latitudinal gradients may lead to wide variation in bioclimatic productivity and other conditions experienced across the range of a species, with stronger seasonality in northern climes and more dramatic temperature variation at higher elevation, conditions nevertheless remain rather predictable at the level experienced by a given population (Willig et al. 2003, Lisovski et al. 2017). However, when comparing species across areas where resources are spatiotemporally unstructured to more structured and predictable environments, dramatically different life history strategies may manifest as evidenced by the migration strategies of giant tortoises (*Chelonoidis* spp.; Bastille-Rousseau et al. 2017). Phenotypic plasticity enables life-history characteristics to exhibit year-to-year variation around a long-term mean as well as spatial variation across a species' range in response to localized pressures (e.g., predation, density dependence; González-Suárez and Revilla 2013, Bischof et al. 2018, Kvile et al. 2021). Yet, that flexibility will be limited by physiological constraints, which themselves change on an evolutionary time scale (Ricklefs and Wikelski 2002). Consequently, alterations to the predictability of resources brought about by land use and climate change may outpace what a species can adaptively compensate for (Boyce et al. 2006). Given rapidly changing environmental conditions, it is therefore incumbent upon wildlife managers to adjust potential limiting factors under their control, e.g., harvest and land management, to ensure species adaptive potential into the future (Regehr et al. 2017, Weiskopf et al. 2019).

Life-history theory may help anticipate how vital rates may change under novel environmental conditions (Barshep et al. 2017, Bellier et al. 2018). For example, those vital rates most influential in driving population growth (i.e., high elasticity) should exhibit the lowest variance over time to buffer the species from unfavorable conditions (Pfister 1998, Morris and

Doak 2004). Further, intraspecific variation in vital rates is expected due in part to heterogeneity in individual condition (Paterson et al. 2018, Badger et al. 2020) combined with differences in habitat quality at the scale of individual home ranges (Bellier et al. 2018). Individuals should choose habitats that confer the greatest fitness returns, assuming unfettered access and accurate knowledge of habitat quality (Fretwell and Lucas 1970). Decreases in fecundity or survival rates, or unfavorable shifts in age structure, such as an increase in non-reproductive juveniles, are population-level consequences of occupying low-quality habitat (Gamelon et al. 2016). Heterogeneous landscapes likely contain a suite of so-called source conditions (where recruitment exceeds mortality) as well as population sinks (where mortality exceeds recruitment), with populations persisting in sinks only from the contributions of immigrating individuals (Pulliam 1988, Pulliam and Danielson 1991). As a result, demographic rates, and subsequently, population growth, often vary across a species' range (Bolnick et al. 2011). Understanding the scale over which vital rates remain relatively constant, and isolating the drivers of variation in vital rates, is needed to elucidate ecological plasticity and, by extension, the adaptive potential of species while also providing the practical, targeted information required for effective species conservation across human-altered landscapes.

### **THE FISHER AS A FOCAL SPECIES IN THE NORTHEAST**

This dissertation focuses on the drivers of, and variation in, vital rates of fisher (*Pekania pennanti*) across a putative gradient of stable and declining populations. Fishers are medium-sized carnivores in the weasel family. Fishers fall towards the slower end of the pace-of-life continuum with many slow-tempo characteristics (e.g., late sexual maturity, long inter-birth interval; Ferguson and Larivière 2002), fishers breed in the spring, exhibit a delayed

implantation strategy, and after a 40-day gestation period give birth the following spring (Frost et al. 2005). Globally, fisher range spans much of the boreal forest in Canada, extending coast-to-coast and southward into the northern United States in the east and mid-west as well as mountainous regions of western states. Across this range, fisher populations have exhibited both widespread expansion in recent decades as well as regional declines (Lewis et al. 2012, LaPoint et al. 2015). Fishers, like many other mammalian carnivores, suffered severe range contractions after the arrival of Europeans in North America due to a combination of deforestation and heavy trapping (Aubry and Lewis 2003, Lewis et al. 2012). Only within the last 75 years, and often as a result of translocations and reintroductions (Lewis et al. 2012), have fishers begun recolonizing their former range (Krohn 2012). Compared to the western United States, the rate of fisher population expansion in the northeastern states has been high and their current range is approaching its pre-colonial extent (LaPoint et al. 2015). In the northeastern states, fisher recovery has been facilitated by regrowth of the region's forest cover over the past century coupled with implementation of sustainable harvest management via regulated trapping seasons (Lancaster et al. 2008, Fuller et al. 2016).

Contemporary forests in the Northeast differ considerably from their historic counterparts. Eastern forests have experienced shifts in canopy species dominance due to a series of disease and pest outbreaks and are now also experiencing shifts in species composition driven by climate change (Bose et al. 2017). Despite an increase in total forest, fragmentation has also increased (Adams et al. 2019), and the Northeast contains extensive wildland-urban interface (WUI; developments adjacent to wild vegetation), with some areas having as much as 84% of housing units located with WUI (Radeloff et al. 2005), and with a continuously expanding urban footprint (Shifley et al. 2014). Such fragmentation and human encroachment also leads to



increased conflict between humans and wildlife (Prugh et al. 2009), with wildlife “spilling over” into residential and agricultural areas, and with toxic residues (Köhler and Triebkorn 2013, Rattner et al. 2014), domestic animals (Brearley et al. 2013, Hassell et al. 2017), and humans themselves (Grignolio et al. 2011, Coppes et al. 2017) spilling over into wildlife habitats. While such altered landscapes are often viewed negatively, tolerance for human disturbance varies among species and type of disturbance, restricting available habitat for some species more than others (Lesmeister et al. 2015). Certain species, including fishers, have adapted (Randa and Yunker 2006, LaPoint et al. 2015) or even responded favorably. Timber harvest and land use conversion has resulted in forests predominately composed of early- to mid-successional stages (Thompson et al. 2013). Early-successional forests often have some of the highest biological diversity (Swanson et al. 2011), and therefore may offer greater prey abundance or diversity. Given the largely shifting and human-dominated forest landscape, it is not surprising that even within a given state, where fisher management has been harmonized, fisher may be rapidly recolonizing parts of their former range while exhibiting evidence of decreasing density in other areas (New York State Department of Environmental Conservation 2015).

## **DISSERTATION ORGANIZATION AND CHAPTER OBJECTIVES**

The following dissertation blends aspects of landscape ecology and population biology, involves multiple sources of data (e.g., camera traps, harvest records, radio-collared individuals) collected over multiple spatiotemporal domains, and tracks the fate and reproductive success of radio-collared individuals across an area spanning the central Adirondacks (low density population) to the Tug Hill (high density population). By quantifying local patterns of fisher vital rates and examining prevalence of an emerging threat to wildlife (i.e., anticoagulant rodenticides) across

landscapes ranging from forest-dominated protected areas (northern NY) to agricultural:forest matrix (southern and western NY), I explored drivers of and variability in fisher vital rates so as to guide effective management action in this heterogeneous and human-dominated region.

Research objectives are organized as distinct dissertation chapters and intended as discretely publishable units and have their own literature cited sections. As such, I use ‘we’ to describe the collective efforts that contributed to this dissertation, though I am the primary author for all chapters.

### ***Chapter 2***

Here, I attempted to determine minimum number of cameras needed to obtain a 95% probability of detection when a female fisher moves kits to a new den. I conducted a field trial and compared the results to preliminary data from five denning female fishers. This chapter was published in *Wildlife Society Bulletin* in 2022 with coauthors Tim Pyszczynski, Tim Watson, Rachel Bakerian, Paul Jensen, and Jacqueline Frair (DOI: 10.1002/wsb.1371).

### ***Chapter 3***

My objective for this chapter was to document prevalence and types of anticoagulant rodenticide compounds in harvested fishers, and to relate ecological and anthropogenic correlates of exposure to number or type of compounds detected per individual.

### ***Chapter 4***

Here, I used radio-collared fishers of both sexes and two age classes (juveniles and adults) to investigate annual survival and cause-specific mortality across northern New York, with Tug Hill Plateau and Adirondack Park serving as focal areas. I explored relationships between environmental gradients, including spatial variation in human encroachment into forest habitats, and stage-, sex- and cause-specific mortality.

## ***Chapter 5***

In this chapter, I investigated kit production and survival until weaning (approximately 10 weeks) along a gradient from the Tug Hill Plateau (high density population) to the Adirondacks (low density population). I explored the role of female den attendance and home range patterns as measures of foraging effort.

### **FUNDING AND PERMITS**

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## **CHAPTER 2: DETECTING DENNING BEHAVIOR WITH CAMERA TRAPS: AN EXAMPLE WITH FISHERS**

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### **ABSTRACT**

Camera traps are often used to monitor wildlife occupancy and, increasingly, to record life history events. For tree-denning species such as fishers (*Pekania pennanti*), camera traps have been used to investigate reproduction (e.g., litter size and kit survival) by documenting females with kits as they move between trees. Yet, unbiased quantification of litter size and kit survival likely requires consideration of detection probability during transitions. We conducted a field experiment with the objective of estimating detection probability of fishers coming to or going from a central tree given different camera arrays and compared that to observations of collared females denning in northern New York. We estimated detection probability via logistic regression and investigated the effects of movement differences related to leaving vs. returning to the tree, as well as temporal effects related to kit development. The number of cameras deployed strongly influenced detection probability, which on average ranged from 0.21 with one camera to 0.85 with 6 cameras, yet detection rate of fishers returning to the den was consistently higher than fishers leaving. Despite the difference in detection relative to direction, we obtained at least one photo of 94% of expected kit transfers. Our results demonstrate the benefits and challenges of purpose-specific tests when using camera traps for estimating demographic rates,

and we offer considerations for researchers that may be considering trade-offs between number of cameras and different collar technology in understanding reproductive ecology of fishers and similar arboreal-denning carnivores.

## **INTRODUCTION**

Camera traps offer an efficient means for surveying a large area for extended periods of time under a vast range of conditions (Silveira et al. 2003, Wearn and Glover-Kapfer 2019), and have been used to estimate and understand distribution (Tobler et al. 2015), population size (Bengsen et al. 2011), activity patterns (Caravaggi et al. 2017), demographic rates (Bridges et al. 2004, Gardner et al. 2010), and niche partitioning (Frey et al. 2017). While there is some evidence that wildlife are aware of camera traps (Meek et al. 2014), they still offer a minimally intrusive option for monitoring aspects of wildlife biology and ecology (Blount et al. 2021).

One consideration in the deployment of remote cameras is the issue of imperfect detection, i.e., false negatives, which when unaccounted for can lead to bias and spurious ecological inference (Guillera-Arroita et al. 2014, Kellner and Swihart 2014). Several factors, including site set-up (Kays et al. 2020), environmental conditions, and behavior of the subject species, can influence detection (O’Connell et al. 2006). Small-bodied wildlife (e.g., 4.8–7 kg) may be missed because they do not enter the camera’s detection bands (Tobler et al. 2008, Urbanek et al. 2019) or are small enough such that the effective detection distance is greatly reduced (Hofmeester et al. 2017). Functionality of camera traps or image quality may be impacted by weather conditions, such as temperature and precipitation (Findlay et al. 2020). For example, falling snow may settle on the front of the camera, obscuring the PIR sensor or lens. Heavy rainfall can decrease the detection distance of cameras (Rowcliffe et al. 2011) and thick

vegetation can lead to a substantial reduction in detection for a variety of species (Moll et al. 2020). Thus, the optimal design of camera arrays is likely to vary according to target species, location, and study objectives (Burton et al. 2015, O'Connor et al. 2017).

Herein, we evaluated the efficacy of remote cameras for capturing fishers (*Pekania pennanti*) departing from and returning to reproductive dens. Fishers are mesocarnivores native to northern and higher elevation forests of North America (Aubry and Lewis 2003, Lancaster et al. 2008) and understanding demographic rates is important for population management. Female fishers use cavities in large-diameter trees to protect kits, periodically moving kits to a new den cavity, using as many as 5–7 trees in the 10 weeks between birth and weaning (Arthur and Krohn 1991, Paragi et al. 1996). Energy expenditure of lactating fishers likely increases 2–3 times that of non-reproductive periods, increasing need for higher-frequency foraging bouts (Powell and Leonard 1983). Therefore, we expected a female would leave their den at least once every 1–2 days.

Traditionally, kit counts have been obtained by cavity checks (Arthur and Krohn 1991, Paragi et al. 1996), but remote cameras have been increasingly used because movement to new dens presents opportunities for non-invasive monitoring (Green et al. 2017). Several researchers have incorporated remote cameras in studies of fisher reproduction and denning behavior (e.g., Jones et al. 1997, Matthews et al. 2013, Green et al. 2017, 2018), yet there have been few explicit attempts to quantify detection of females leaving and returning to den trees (Cummins 2016, Smith et al. 2020). Smith et al. (2020) estimated the minimum proportion of missed detections based on the assumption that a female left or returned to the den at least once every day, and detected female fishers on 71–73% (95% CI = 66% – 78%) of days the dens were monitored. Cummins (2016) estimated litter size at 43 dens using remote cameras (3 at each den)

and data loggers that recorded pings from VHF collars when the females were nearby. Cummins (2016) found that data loggers detected kit moves at 67% of dens, while cameras detected kit moves at only 51% of dens, and at dens where both methods detected kit moves the same number of kits were detected only 72% of the time. Therefore, questions remain regarding how well detection probability can be quantified and corrected for when monitoring den trees.

The overall objective of our study was to determine the minimum number of cameras necessary to achieve a 95% probability that we would capture a female fisher as she moved kits between den trees. Toward that end, we first designed a field trial that would mimic fisher den tree activity. We baited fisher to a central tree surrounded by 15 equally spaced cameras, enabling us to establish events when the fisher was within the camera array (true events) and the probability of detection given a decreasing number of cameras. To test applicability of our field trial, we also estimated camera detection probability of female fishers at reproductive dens, using activity data from collared females as a means of verifying camera observations *in situ*. We predicted that detection would increase asymptotically with the number of cameras, and predicted that >3 cameras would be necessary to capture at least 95% of movements in the field trial and at den trees the field trial and at den trees. We considered 95% to be a sufficiently high detection rate to be confident in attendance patterns and kit counts, while allowing for some error. At den trees, we also predicted that the direction that the fisher was moving (i.e., leaving or returning to the den) would influence detection rates, and that detection of kit movements would increase with time as kits grew in size.

## STUDY AREA

Fisher live-trapping and reproductive den monitoring occurred in 2 study areas in northern New York, including the Tug Hill Plateau (2,287 km<sup>2</sup>) and central Adirondack Mountains (9,506 km<sup>2</sup>). Elevation ranged from 200–610 m on the Tug Hill, and 400–1,600 m in the Adirondacks. We conducted the field experiment in the Happy Valley Wildlife Management Area (WMA), located on the southern edge of the Tug Hill Plateau (elevation approximately 200 m), but outside of the live-trapping study area. Happy Valley WMA was a 36 km<sup>2</sup> natural recreational area managed by the New York State Department of Environmental Conservation (NYSDEC). We selected this location for the field experiment because we expected it to have a relatively high-density fisher population (Linden et al. 2017) to increase the potential opportunities of obtaining a sufficient number of observations of fishers at baited locations.

Study areas contained a mix of private and public forestland. In general, northern New York is comprised of northern hardwood, spruce-fir, or hardwood/spruce forest types (Bryce et al. 2010). Dominant species across both study areas included sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*), however the forest composition shifts to a higher proportion of pines and spruces (e.g., red spruce [*Picea rubens*] and white pine [*Pinus strobus*]) as elevation increased in the Adirondack Mountains. Stand age was generally younger in the Tug Hill than Adirondacks (McGee et al. 1999, Pan et al. 2011), with a greater proportion of public land protected from development in the Adirondacks (i.e., Adirondack Park; Kretser et al. 2008). Herbaceous understory coverage was variable in northern New York, and could be negatively associated with high-density overstory, which was more common in unharvested stands (Woodcock et al. 2008). On average, vegetation leaf out began slightly earlier in the Tug Hill

study area (17–28 April) than in the Central Adirondacks study area (20 April–7 May; USA National Phenology Network 2017).

Mean annual temperature was 6.8° C for the Tug Hill and 6.2° C for the Adirondacks (Northeast Regional Climate Center 2021). The Tug Hill region of New York experienced frequent and intense lake-effect snow events, with average September–May snow totals that often reached 500 cm, though the occurrence of these events generally decreased after January (Veals and Steenburgh 2015). The Adirondack Park received up to 350 cm of snow on average (Glennon and Porter 2007).

## **METHODS**

### ***Field experiment***

Between 31 January and 12 March 2020, we deployed a total of 45 RECONYX® Hyperfire 2 Covert (RECONYX Inc, Holmen, WI, USA) cameras across 3 stations. The first station was deployed on 31 January, while the remaining 2 were deployed on 12 February 2020. General location of stations was selected based on researcher access and for topographical characteristics that were suspected to facilitate movement of fishers. We selected focal trees based on characteristics of den trees used by female fishers, for example, trees with a large diameter ( $50 \pm 11$  cm) or evidence of decay/damage (Paragi et al. 1996, Weir et al. 2012). We also selected for trees that were at least 85% clear of vegetation within a 5 m radius to ensure visibility. Stations were 0.5–2.3 km apart. At each station, 15 cameras were placed facing inwards 4.8–5 m from the tree at 24° intervals in a circle around a single focal tree. We expected that 15 cameras would oversaturate the area around the tree, preventing any blind spots in visibility. If camera view of the focal tree was impeded, the camera was shifted within 1 m so that the focal tree would be

visible. Cameras were positioned on existing trees within 5 m of the focal tree when available or otherwise on metal fence posts. Cameras were positioned facing the focal tree such that the camera captured the base of the tree as well as the ground around the tree, without angling the cameras. As a result, height of camera placement varied with ground topography.

We used beaver (*Castor canadensis*) meat and Gusto carnivore lure (Caven's Predator Lure, Pennock, MN, USA) to attract animals to our camera arrays. Beaver meat was attached to the tree with 2.54 cm poultry fencing and 3.35 kg 16-gauge tie wire opportunistically in 1–3 areas, at approximately 0°, 120°, and 240°. If only one piece of bait was used, bait was placed at 0°. If 3 pieces of bait could not be placed, a small amount of lure was smeared on the tree in locations where there was no bait. Bait and lure were placed approximately 1.5 m from ground level. Cameras were programmed to take 3 photos at 1-second intervals with each trigger of the motion sensor, which was set to the default high sensitivity setting. We checked cameras every 7–10 days to download photos, replace batteries, and refresh bait and lure. We reviewed photos after downloading to assess camera placement and repositioned cameras if the view of the tree appeared skewed.

### ***Fisher capture and den monitoring***

We used Tomahawk box traps model 108 (Tomahawk Live Trap, Hazelhurst, WI, USA) to capture fishers between 25 October 2019 and 6 March 2020. Traps were baited with beaver or moose (*Alces alces*) meat, insulated with sheep's wool and corrugated plastic sheeting, and checked at least once every 24 hours. Fishers were immobilized via intramuscular injections of ketamine hydrochloride (25 mg/kg; Zoetis, Parsippany, NJ, USA) and xylazine hydrochloride (5 mg/kg; ZooPharm, Fort Collins, CO, USA), and after processing the animals we administered

yohimbine (0.15 mg/kg; ZooPharm) or atipamezole hydrochloride as an antagonist to the xylazine (1 mg per 10 mg xylazine given). Adult females (i.e., estimated to be  $\geq 1.5$  years old) were fitted with Lotek LiteTrack RF 40 GPS/VHF collars with swift fixes enabled (Lotek Wireless, Newmarket, ON, Canada), which collected location fixes every 3 hours between 21 February and 31 May. Each GPS collar included a temperature sensor and a tri-axial accelerometer which recorded data summarized over 2 axes at 5 min intervals. Sensors were active between 1 March and 31 July.

After 6 March, we located collared fishers via radio telemetry 2–3 times per week to identify reproductive dens (Figure 1). We began monitoring near the fisher's last known location using an omnidirectional VHF antenna mounted to the roof of a vehicle. Individuals that could not be located from the ground were searched for using a pair of 4-element Yagi antennas mounted to a fixed-wing aircraft (Cessna 172, Wichita, KS, USA). When a signal was detected, we located the fisher using the VHF signal and noted if she was moving or in a tree, and downloaded location and activity data from GPS collars if possible. If a fisher was located in the same tree for  $\geq 2$  days (Paragi et al. 1996, Green et al. 2017) we set up to 6 Reconyx Hyperfire 2 Covert camera traps facing towards the den tree at distances between 4–7 m. The number of camera traps placed was determined by the number of cameras available and the researcher's determination of what would be sufficient to capture the full field of view around the den. Cameras were affixed to trees surrounding the suspected den tree at heights of approximately 0.5–1.2 m, programmed to capture 3, 5, or 10 consecutive photos with sensitivity set to high, and were checked every 2–10 days. Frequently, we set 1–3 cameras on the initial visit, with additional cameras added on subsequent visits after confirmation that the tree was being used as a den. If no kits were observed in photos or no photos were present after several days, we



restarted the search process for a new den using the previously described telemetry techniques. We continued to locate new den trees until kits were weaned and traveling with the adult female, generally by early to mid-June (Powell 1993), after which time observing kits becomes substantially more difficult (Aubry and Raley 2006).

Given that the GPS data we collected were temporally too coarse (i.e., every 3 hours) to provide a definite indication of whether a fisher was at the den and fix success rate for GPS collars during the study period was 36%, we relied on only activity data from the collar accelerometers. We combined the 2 axes into a single metric by computing the square root of the summed square of both axes (Qasem et al. 2012). Expecting dens to be warmer than the outside air temperature, we classified activity data into active and inactive periods using K-means clustering and 3 variables: activity value at time  $t$ , activity value at  $t-1$ , and collar-measured temperature—each standardized to have a mean of 0 and standard deviation of 1. Ultimately, we located points in the activity data that switched from active to inactive or vice versa to delineate distinct event periods that, in combination with camera data, would allow us to delineate if the female was in or away from the den.

### ***Processing camera data***

We used digiKam software (version 6.4.0, [www.digikam.org](http://www.digikam.org), accessed 1 March 2020) to write tags to the photo metadata, which included information on species, direction of movement, and the presence of a GPS collar and whether a kit was detected (reproductive den monitoring only). We classified photos of the female as either leaving or returning based on the direction she was facing or moving, using the entire photo sequence where possible to identify movement direction. A subset (~50%) of photos from the field test were reviewed by a second observer to

confirm consistency and accuracy of the image tagging, as were movement directions and all photos of kits. We used the packages `exifr` (Dunnington and Harvey 2019) and `camtrapR` (Niedballa et al. 2016) to extract photo metadata information and tags for import into Program R (v. 4.1.0; R Core Team 2021) and filtered the dataset to only include photos of fishers (field experiment), or only fishers with collars (reproductive dens). If the animal's neck was not visible, we examined the photos to gauge body size of the fisher, and if it was similar to that of known females, we included those in the data set unless activity data indicated that the female fisher was away from the den.

We grouped photos into 1-minute intervals using the `spatsoc` package (Robitaille et al. 2019) for both the field experiment and reproductive den monitoring. In the field experiment, we defined an event to be any 1-minute interval in which at least one of the 15 cameras detected a fisher. Because animals visited and fed at our baited stations, 90% of events occurred within 4 minutes of the previous event. Assuming these temporally concentrated events to be part of the same visit, we constrained the recording of a new visit only after >25 minutes had passed since the previous event. Because we were interested in measuring detection for more ephemeral events, such as a female fisher moving kits down and away from the den tree, for each visit we retained only the first and last detected events (i.e., coming to or leaving the site).

To test alternative camera configurations with our field experiment, we virtually rarefied the 15 cameras used in the field trial to 6 cameras and established a set of 47 possible combinations of 1–6 cameras. We restricted our combinations to a maximum of 6 cameras, given that the use of more devices under a typical field study would be unlikely (Whytock et al. 2021). Therefore, for each event in which at least one photo was taken, there were 47 possible observations. Because the direction of the female after leaving or returning to the den would

likely be unknown, full-circle coverage was desired over a single direction, and thus our virtual combinations only included evenly spaced arrangements of cameras. We censored camera combinations that were covered by snow (when the motion sensor was triggered, but photo was obscured), if the camera placement was such that the tree was not in the center of the field of view (i.e., in the outer quarter of the frame on either side), or due to battery failure or camera malfunction.

To analyze detections at reproductive dens, we aligned activity with labeled photo captures based on time (Figure 2). To identify missed detections, we identified time points where we expected a photo based on transitions in activity and previous detection. For example, if 2 consecutive photos captured several hours apart showed the fisher returning, and if the activity data indicated a transition between active and inactive states, we inferred that we missed a detection of the female leaving the den. We counted the number of kits moved by each female at each den in order to quantify the proportion of kit transfers captured on camera.

We removed observed instances of the female leaving the den and then returning in <10 minutes from the analysis because we were not confident in determining missing photos, because activity data did not always indicate a transition between inactive and active. Further, we excluded any photographs of the female fisher interacting with males, as we expected behavior to be different during interactions. We did not include data from one den for which we could not verify that the den was used for reproduction (rather than as a rest site) or confirm the endpoint of den use. Though kits were heard on one visit, we detected the female visiting this den on only 3 occasions over 2 weeks, and in each series of photographs she appeared to be moving away from the tree while the activity data indicated that it was near the end of an active period. For the

analysis of detection at den trees, we also excluded days from the dataset during which kits were moving under their own power.

### *Statistical analysis*

To investigate the relationship between the number of cameras and detection probability for fisher at reproductive dens and field experiment sites, we used logistic general linear mixed models (GLMMs) in R using the package lme4 (Bates et al. 2015) and summarized coefficients with the broom.mixed (Bolker and Robinson 2021) and performance (Lüdecke et al. 2021) packages. For the field experiment, we tested the effect of number of cameras on the probability of at least one photo being captured in an event, and we included a random effect for each event (i.e., when at least one photo was captured). At the reproductive dens, we examined the additive and interactive effects of type of activity (i.e., leaving or returning) and week of denning period on detection rate. We included a random intercept for each den to account for variability in individuals and sites. We used package MuMIn (Barton 2020) to rank models according to Akaike's Information Criterion for small sample sizes ( $AIC_c$ ) and considered models with  $<2 \Delta AIC_c$  to be competitive (Burnham and Anderson 2002). We standardized continuous covariates to have a mean of 0 and standard deviation of 1.

## **RESULTS**

Photo tags were largely in agreement between initial and second observers for both the field experiment and analysis of reproductive dens. In the reproductive den photos, the second observer identified 2 instances of a prey item being mislabeled as a kit, as well as one instance where the kits were not noted by the first observer.

We obtained 41,962 photos of fishers between 31 January and 12 March 2020. After classifying unique visits and extracting the start and end point of each visit as distinct events (based on records of all 15 cameras combined), we identified 172 independent events (i.e., 1-minute intervals with at least one photo captured separated by at least 25 minutes) for comparison to alternative camera deployments. Detection probability ranged from 0.21 (95% CI = 0.17 – 0.25; one camera) to 0.85 (95% CI = 0.81 – 0.88; 6 cameras). Our model indicated that the odds of a fisher being detected increased by 2.84 (95% CI = 2.63 – 3.08;  $P < 0.001$ ) with an increase of 1 standard deviation in number of cameras. The variance of the random event effect on the logit scale was 2.09, indicating high variability between events (baseline detection probability for 95% of events was between 0.07 and 0.96). Additionally, the conditional  $R^2$  (0.49) was substantially larger than the marginal  $R^2$  (0.17), providing further evidence that much of the variation in the data was explained by the random effect (Nakagawa and Schielzeth 2013).

We monitored 5 collared and denning female fishers across 16 reproductive dens between 20 March and 5 June (spanning 12 weeks). We monitored an additional 6 trees as potential dens, but each was later determined to be rest sites due to lack of repeated use by the females. The number of reproductive dens per female was on average 3.2 (range 2 – 4), and females used a given den for a period of 1.2 to 36.2 days. We analyzed 51,985 photos during the denning period. We identified 367 known events, i.e., sightings of the collared female returning to ( $n = 226$ ) or leaving ( $n = 141$ ) the den. The sequence of events revealed 37 returning and 138 leaving events that the cameras failed to capture. We observed females with either 2 (3 of 5 females) or 3 kits (2 of 5 females). Kit counts were consistent for all females across all dens where kits were detected, except for 2 instances in which we counted one fewer kit at the last den. At one den, we obtained a photo of the female leaving the den again several hours after moving the first kit, and it was

unclear if she moved a second kit. At the second, we were unable to infer from activity data whether the female returned to the den to retrieve the last kit, and additional den trees could not be located. Overall, we obtained photos of 94% of expected kit transfers.

In addition to the top model, 2 models in our candidate set had a  $\Delta AIC_c$  value  $< 2$  (Table 1). The top model included additive effects of number of cameras and type of movement, while the next best model included the interactive effects of the same covariates. The third model included an additive effect of week in addition to number of cameras and type of movement. The interaction term of the second model and the week covariate in the third model did not receive statistical support. We considered these terms to be uninformative parameters, which would suggest that the cumulative weight of number of cameras and type of movement approached 1 (Arnold 2010). Therefore, we reported parameter estimates from only the top model. The odds of a fisher being detected increased by 1.93 (95% CI = 1.34 – 2.76) when increasing by 1 standard deviation in number of cameras, and the odds of detection increased by 0.12 (95% CI = 0.07 – 0.19) for returning compared to leaving the den. The estimated probability of detection ranged between 0.17 (95% CI = 0.06 – 0.39; one camera) and 0.81 (95% CI = 0.62 – 0.91; 6 cameras) for fishers leaving, and between 0.64 (95% CI = 0.37 – 0.85; one camera) and 0.97 (95% CI = 0.91 – 0.99; 6 cameras) when they returned (Figure 3). The variance of the random intercept for den on the logit scale was 1.14, indicating moderately high variability (baseline detection probability for 95% of dens was 0.54 – 0.99). The proportion of the variance explained by the entire model was 0.46 (conditional  $R^2$ ), while the proportion of variance explained by just fixed effects was 0.27 (marginal  $R^2$ ).

## DISCUSSION

Appropriately accounting for imperfect detection is often a critical component of wildlife surveys and research (MacKenzie et al. 2002, Lahoz-Monfort et al. 2014). Our objectives were to determine the number of cameras necessary to achieve a desired detection probability for fishers and fishers with kits. By attracting fishers to a focal tree using bait, we found detection probabilities increased from 0.21 to 0.85 by increasing the number of cameras from 1 to 6. However, even 6 cameras were insufficient to achieve a 95% detection probability. Previous studies have typically used 2 – 4 cameras for monitoring fisher dens (Matthews et al. 2013, Sweitzer et al. 2015, Facka et al. 2016, Green et al. 2018, Smith et al. 2020). Our analysis of cameras placed *in situ* at reproductive dens paired with estimates of fisher activity from collars corroborated the positive effects of adding additional cameras. However, they revealed a consistently and substantially lower detection probability for females departing from their dens (0.56 – 0.70 for 4 – 5 cameras) compared to returning to them (0.92 – 0.95). Such low detection rates initially appear to be concerning when the goal is to assess kit production, yet we captured photos of 94% of expected kit transfers, suggesting that the rate of capturing kit moves is greater than that of females leaving the den unencumbered.

Consistent with previous studies (Larrucea et al. 2000, Rowcliffe et al. 2008), our results indicated that detection probability is driven in part by behavior of the individual in relation to the detection band of the cameras. Most trail cameras operate with a passive infrared (PIR) motion sensor, which detects thermal differences if the animal occurs within the camera's detection band (Apps and McNutt 2018a). We suspect that a female's greater momentum when going down versus up a tree, combined with the likelihood of her leaping off the tree near the bottom, may have allowed her to move out of the field of view quickly without crossing enough

of the detection bands to reliably trigger a camera. We also observed the female fishers climbing and descending trees adjacent to the den tree. When transferring dependent kits from one tree to another, females must carry them in their mouths, which from our photos and videos is an arduous and awkward process. Females carrying kits are likely to move slower down the bole of the tree, and unlikely to leap from the tree at risk of dropping or injuring the kit. Further, we observed females leaving from the actual den tree, rather than an adjacent tree, when moving kits. Our photos also indicate the potential need for females to stop at the base of the tree to readjust their hold on the kit before continuing away from the tree, which likely offers a much greater opportunity for camera detection of females while moving kits.

Though our results showed a clear increase in detection with an increase in the number of cameras, we suspect that strategic placement of cameras is potentially just as important. The cameras used in our study have a field of view of 40° (Reconyx 2018), suggesting that 9 cameras would be required for full 360° coverage. Yet, when we observed kit moves, there was an average of 4.5 cameras set at the dens, and at least one photo was captured by an average of 2.6 cameras. Typical of other studies employing camera traps to assess reproduction in fishers, our field crews surveyed the den tree and surrounding structures for possible den entrances and travel routes before setting cameras. The quick movements of the unencumbered female may still be too fast for the camera sensors even with full coverage, and so we suggest that some cameras be placed further out from the den (i.e., beyond 5 – 7 m), especially if a travel route can be identified, to increase detection related to den attendance.

Based on previous research (Smith et al. 2020) we had predicted a temporal trend in detection rates due to seasonal changes and kit growth. Yet, we did not observe any temporal effects on detection. We had predicted that activity of the female might be obscured by



vegetation later in the denning season. However, much of our study was conducted prior to spring green-up, and the majority of photos captured had minimal herbaceous vegetation obscuring the den tree or the ground around it. During the 12-week study period, we noted one instance where we could not confidently count the number of kits emerging from a den in late May due to green vegetation, though we excluded this event from our analysis because kits were moving independently and not carried by the mother. However, assessments of kit survival could be impacted by a lack of certainty due to dense vegetation at the end of the denning season.

Pairing activity data from collar-borne accelerometers with camera traps around den trees, proved useful in interpreting how much behavior might be capturable by cameras, and can provide insight into den attendance rates and foraging time (i.e., duration of time required away from the den for hunting). Female fishers display behavioral changes during the denning season, in which they abruptly shift from widespread movements to a confined area of their home range when they establish a natal den (Matthews et al. 2019), and they spend considerably more time at the den when kits are very young (Cummins 2016). The patterns of activity documented by the collars' activity sensors were consistent with those observed by Leonard (1980). Thus, we are confident that our collar data provided a useful estimate on den attendance to which camera detections could be compared. However, our analyses indicate a differential ability to detect returns to compared to departures from the den using camera traps alone, and we are not confident that cameras as deployed in our study would provide an unbiased estimate of fisher activity around the den site, should den attendance patterns be of most interest. Instead, we recommend a combination of cameras and collars equipped with accelerometers.

Our analysis was based on Reconyx cameras, and functional differences in how motion is detected has been demonstrated across different camera manufacturers and models (e.g.,

Weingarth et al. 2013, Wellington et al. 2014). As a result, tests of the cameras to be used in a particular study are essential for fully understanding rates of detection and the factors that may influence them (Urbanek et al. 2019). Controlled trials may be informative as long as the experimental design can replicate the expected field conditions (Apps and McNutt 2018b). We assumed coming and going from a baited tree would approximate female movement coming and going from her den tree, and the field experiment and *in situ* trials corroborated the effect of the number of cameras on detection probabilities. However, animal behavior differs with goal-oriented pursuits, with the goal of eating bait in the middle of the cameras' focal area proving quite different from the goal of climbing quickly up a tree and into a den, or of carrying a kit down and away from the tree.

While we focused our attention on fishers, our investigation and insights may be informative for American marten (*Martes americana*) and wolverine (*Gulo gulo*)—both of which also use dens to protect offspring when they are very young (Magoun and Copeland 1998, Ruggiero et al. 1998). With the increase in the use of camera traps in wildlife research over the past 2 decades (Blount et al. 2021), our results offer encouraging implications for the use of camera traps in monitoring maternal behavior and recruitment rates in elusive forest carnivores.

## **RESEARCH IMPLICATIONS**

Estimating vital rates and subsequent population processes is one of the greatest challenges in wildlife management. Not only do budgetary and logistical constraints often limit the scope and duration of monitoring surveys, but the behavioral characteristics of some species, including small, elusive carnivores make them inherently difficult to monitor. While camera traps offer the means for efficient long-term monitoring, they are still quite costly when used in large quantities.

Therefore, understanding detection rates of a species or event can improve efficiency of study designs, and thereby maximize the utility of funding and personnel. Such estimates of detection can facilitate greater usage of cameras in estimating demographic rates as well as other event-driven studies.

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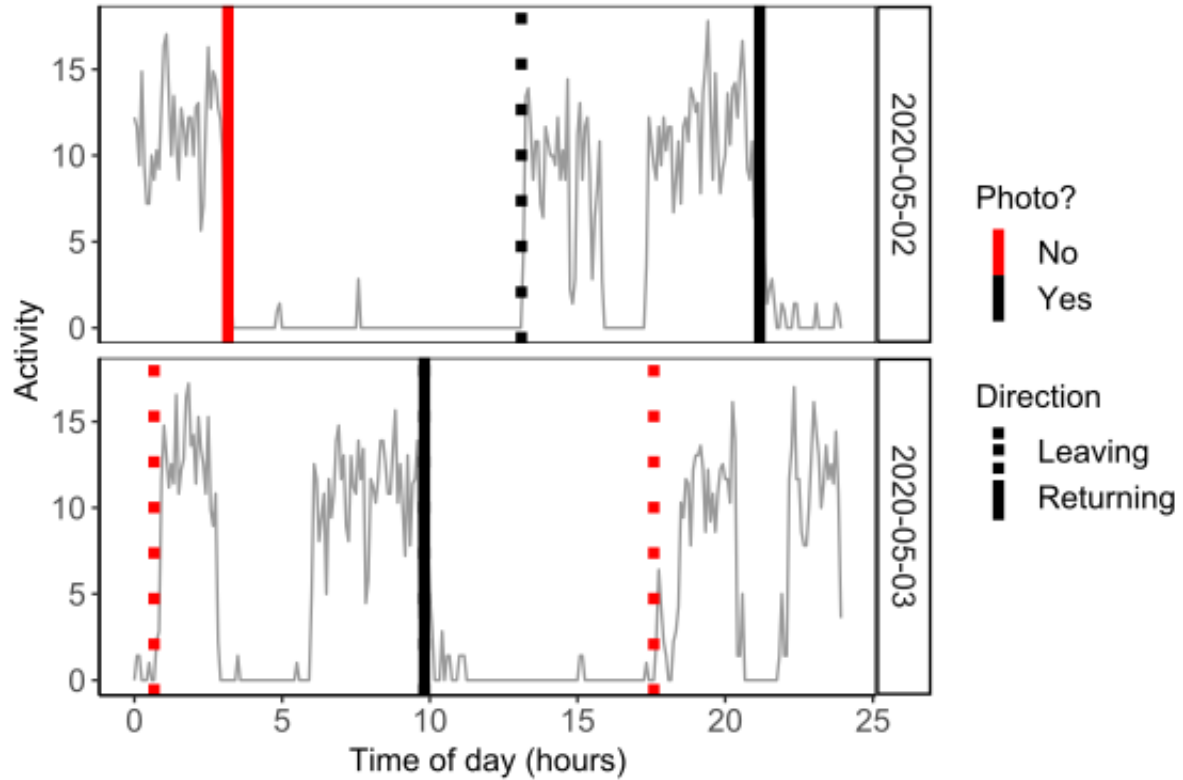


**Table 2-1:** Comparison of candidate models predicting the probability of detection of fisher in situ at reproductive dens in northern New York, USA during the 2020 reproductive season. We show the number of parameters ( $k$ ), log likelihood ( $\log\text{Lik}$ ), Akaike’s Information Criterion for small sample sizes ( $\text{AICc}$ ), difference in  $\text{AICc}$  from the top model ( $\Delta\text{AICc}$ ), and model weight ( $w_i$ ). The binary response was designated as 1 when a fisher was detected by at least one camera, and zero if the fisher was expected (based on GPS and activity data) but not captured by any camera. We included terms for the number of cameras (cameras,  $n = 1 - 6$ ), whether the animal was leaving or returning (movement), week of the denning period (week), and a random intercept for den.

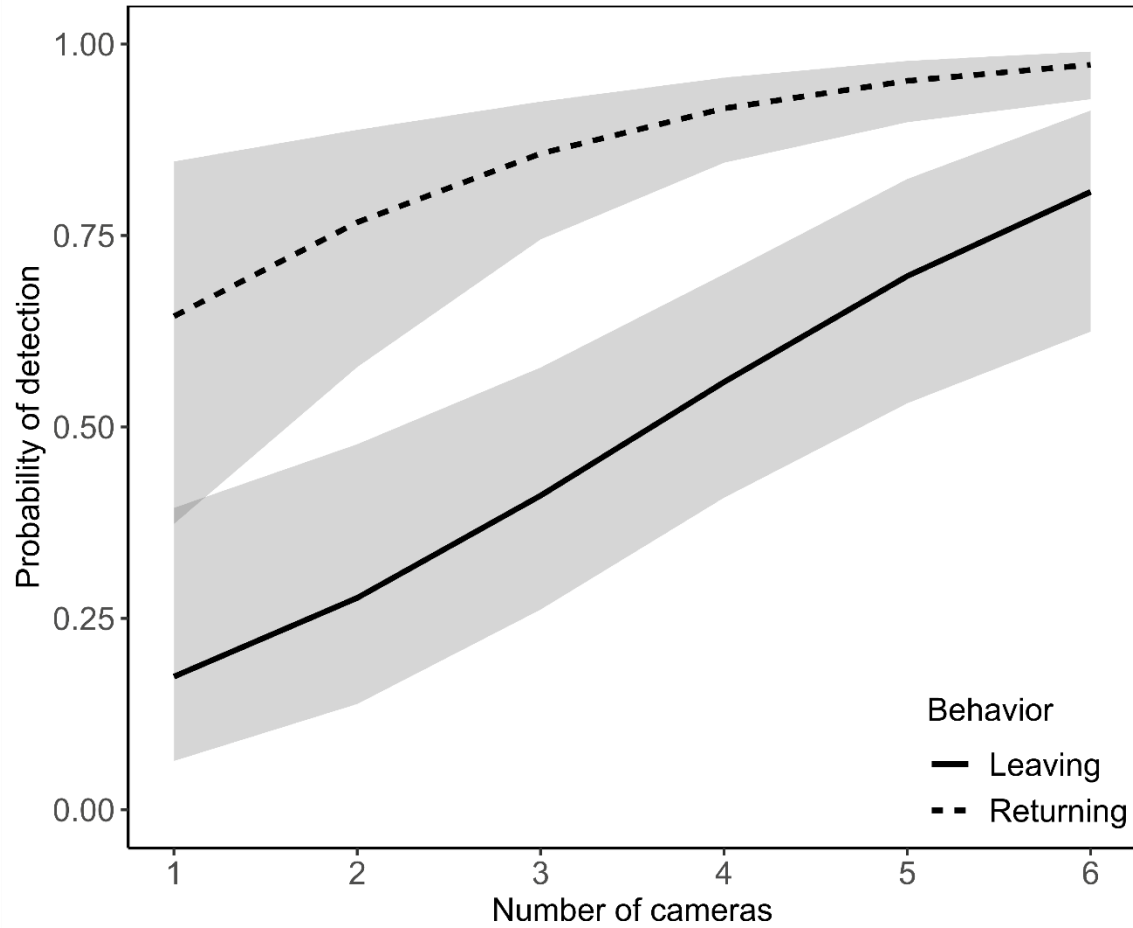
Model	$k$	$\log\text{Lik}$	$\text{AICc}$	$\Delta\text{AICc}$	$w_i$
Cameras + movement + (1 den)	4	-266.6	541.3	0.00	0.57
Cameras $\times$ movement + (1 den)	5	-266.5	543.2	1.88	0.22
Cameras + week + movement + (1 den)	5	-266.6	543.3	2.01	0.21
Movement + (1 den)	3	-273.6	553.2	11.90	0.00
Cameras + (1 den)	3	-314.4	634.8	93.47	0.00
Cameras + week + (1 den)	4	-314.4	636.8	95.49	0.00
Cameras $\times$ week + (1 den)	5	-313.7	637.5	96.25	0.00
(1 den)	2	-320.6	645.2	103.96	0.00
Week + (1 den)	3	-319.9	645.9	104.60	0.00



**Figure 1:** Photo of a collared female fisher (*Pekania pennanti*) moving a kit to a new den captured via camera trap in the Tug Hill region of northern New York, USA in May 2020.



**Figure 2:** Comparison of activity data (collected from a collared fisher) to camera records focused on the den tree over 2 days in May 2020 in northern New York, USA. Activity was measured as acceleration over 2 axes and summarized into a single metric at 5-minute intervals. Values ranged from 0 (no movement) to >15 (high-intensity movement). The vertical lines indicate den departure (dotted line) or return (solid line) events and are color-coded to indicate successful photo capture of the event (black) or a failed detection (red).



**Figure 3:** Predicted probability of detection for 1 to 6 cameras in situ at 16 fisher reproductive dens, in northern New York, USA, March–June 2020. Detection probability was consistently higher when fishers were returning to the den (dashed line) than when leaving.

## CHAPTER 3: SPATIOTEMPORAL DRIVERS OF RODENTICIDE EXPOSURE IN A MAMMALIAN FOREST CARNIVORE ACROSS NEW YORK STATE, USA

### ABSTRACT

Anticoagulant rodenticide (AR) use is the primary method to control rodent pests, but carries a high risk of wild carnivores and scavengers consuming toxic prey. Although point sources are difficult to identify, proximity to agriculture and urban developments correlate with increased AR exposure in non-target wildlife. Yet, in forest-dominated regions ecological processes such as pulsed resources (e.g., mast seeding) influence small mammal abundance, predator movements, and potentially AR use and exposure. We acquired a snapshot of rodenticide exposure within the standing population of fishers (*Pekania pennanti*) from legally harvested individuals ( $n = 338$ ) across New York State over a three-year period (2018–2020), spanning two beech (*Fagus grandifolia*—the primary mast producing species in northern New York) mast events and one mast failure. We modeled the total number of AR compounds an individual was exposed to (representing different exposure events) as well as the probability of exposure to each of the three most detected compounds (brodifacoum, bromadiolone, and diphacinone). We tested whether covariates related to farming, human encroachment into forests, and prey cycles driven by mast seeding were informative regarding AR exposure levels. Overall, we detected residues from 1–5 AR compounds in 83% of sampled fishers, with diphacinone, brodifacoum, and bromadiolone detected in 74, 58, and 30% of samples respectively. Middle-aged animals (e.g., approx. 3.5–4.5 years) were the most likely to be exposed, and males showed greater exposure than females. The proportion of wildland-urban intermix within a 15-km<sup>2</sup> buffer around each sample was positively associated with, and the strongest predictor of, the probability of exposure to both common AR types and the total number of rodenticide compounds in an individual. An

index of beech mast productivity showed a 1-yr lagged effect (increase) on the number of compounds detected overall and 2 common AR types. Our results demonstrate that ARs are ubiquitous across the landscape, from agricultural to forest-dominated landscapes, with household use likely driving the bulk of exposures in non-target wildlife even in particularly remote and protected forest areas. Further research into the risks to wildlife persistence given rodenticide use by private citizens and pest management professionals, as well as the ecology of food availability for predators, will be important to effectively conserving wildlife while securing human safety into the future.

## **INTRODUCTION**

While anthropogenic stressors have negatively impacted wildlife species in a variety of ways (Gaynor et al. 2018, Tucker et al. 2018, Rosenberg et al. 2019, Hill et al. 2020), there are those that thrive in human-dominated environments (e.g., Bateman and Fleming 2012, Fox and Abraham 2017, Tucker et al. 2020). Synanthropic species such as rats (including *Rattus rattus*, *R. norvegicus*, *R. exulans*) and mice (including *Mus musculus*) have excelled at exploiting human-built structures (Weissbrod et al. 2017) and, as a result, have spread and become invasive across the world (Banks and Smith 2015). These species are responsible for spreading disease (Smith and Carpenter 2006, Diagne et al. 2017), damaging crops (Witmer et al. 2000, Witmer 2019), and negatively impacting native biodiversity (Harper and Bunbury 2015). Since the 1940s, anticoagulant rodenticides (ARs) have been widely deployed as the primary method of reducing rodent populations (Watt et al. 2005), being applied in agricultural and urban settings, and used in the removal of invasive species on islands (Howald et al. 2007, Wheeler et al. 2019).

There are several types of ARs available for use globally, with variation among nations in availability and regulations (Jacob and Buckle 2018). ARs are generally divided into warfarin-based first-generation (FGARs) and the more potent second-generation compounds (SGARs; van den Brink et al., 2018). First generation ARs often require multiple doses before an animal accumulates a fatal dose, while SGARs generally deliver a fatal dose in a single feeding (Rattner and Mastrota 2018). In the United States, the Environmental Protection Agency (EPA) has imposed regulations to limit use of SGARs primarily to pest management professionals or agricultural settings, while FGARs are more readily available on the consumer market for household use (Erickson and Urban 2004, U.S. Environmental Protection Agency 2008, Jacob and Buckle 2018). While most ARs are labeled for use indoors or within 50 ft (15.2 m) of buildings, certain FGARs are approved for use in fields (crops and non-crops) and other locations such as train tracks (U.S. Environmental Protection Agency 2008).

Deployment of ARs serves an important purpose for protection of human health and property, but also poses a threat to the health of non-target organisms. Carnivores and scavengers are most frequently exposed by consuming contaminated prey (López-Perea and Mateo 2018), because small mammals suffering from AR poisoning may alter their behavior in a way that increases their vulnerability to predators (Cox and Smith 1992, Erickson and Urban 2004, Hindmarch and Elliott 2018). Poisoned prey may remain alive and available to predators for up to a week after ingesting a lethal dose (U.S. Environmental Protection Agency 2008) before ultimately perishing from spontaneous or trauma-induced bleeding (Rattner and Mastrota 2018), while carcasses of poisoned rodents are also available for scavenging (Montaz et al. 2014). Whereas many rodenticide applications aim to target invasive commensal rodents, several native species are also targeted in agricultural settings (e.g., *Microtus*, *Thomomys*, *Otospermophilus*

spp.; Baldwin 2014, Baldwin et al. 2014, Montaz et al. 2014). Non-target small mammals and passerine birds may directly access bait blocks intended for mice and rats (Hindmarch and Elliott 2018), leading to high exposure rates, and further becoming a source of contaminated prey for mammalian carnivores.

Due to the risk of secondary exposure in carnivorous birds and mammals, numerous studies have investigated the links between landscape characteristics and AR exposure. Worldwide, the risk of exposure to ARs in raptors increases with proximity to agriculture and dense human populations (Hindmarch et al. 2017, Lohr 2018, Pay et al. 2021), and some studies have linked higher exposure rates specifically to livestock production (López-Perea et al. 2019, Rial-Berriel et al. 2021). Mammalian predators also experience increased risk of exposure near urban centers (Riley et al. 2007, Poessel et al. 2015, Serieys et al. 2019) and within agricultural landscape mosaics (Nogeire et al. 2015). Suburban residential areas are sources of ARs (Elliott et al. 2022), especially those in areas adjacent to tracts of forest or open space (Burke et al. 2021). Increasingly, evidence is accumulating for AR exposure on the far end of the urban-forest gradient (Cooke et al. 2022), with evidence of avian (Franklin et al. 2018, Gabriel et al. 2018) and mammalian exposure deep in forests (Gabriel et al. 2012, Thompson et al. 2014). While this may be in large part due to illegal cannabis cultivation (Wiens et al. 2019, Wengert et al. 2021), isolated homesteads or other structures are being recognized as strong contributors (Hofstadter et al. 2021). Thus, in the northeastern United States, where rural human population densities and habitat fragmentation are high relative to the rest of the United States (Shifley et al. 2014, Adams et al. 2019), there is potential for multiple routes and high levels of AR exposure among forest wildlife.



In the forest-dominated northeastern US ecological processes, such as resource pulses that periodically amplify rodent numbers, may intensify the impacts of rodents and drive application of ARs. Mast seeding cycles frequently influence small bird and mammal populations (Clotfelter et al. 2007), with periodic increases in food resources boosting productivity (Ostfeld et al. 1996), or alternatively, in mast failure years, reduced food availability may lead to lower survival or productivity (Schmidt and Ostfeld 2008). Carnivore populations often fluctuate with available prey and experience a similar but lagged response to pulses in prey availability (King et al. 2003, Jensen et al. 2012, Greenhorn et al. 2021). Pulsed resources can lead to human-wildlife conflicts in low resource years when wildlife seek alternative food sources (Bautista et al. 2022). For example, hardwood seeds such as oak (*Quercus* spp.) constitute a sizable portion of black bear (*Ursus americana*) diet, and in mast failure years, human-bear conflicts and road mortalities increase as bears range further to find sufficient food and increase their use of human food sources (Ryan et al. 2007). Rodents and their predators in the northeastern United States depend on the masting cycles of several deciduous species (McShea 2000), but the link between AR exposure and mast cycles has not been explored in this region. In European agricultural landscapes, periodic vole (*Microtus arvalis*) outbreaks have been associated with higher AR exposure in weasels (*Mustela nivalis*; Fernandez-de-Simon et al. 2022). Therefore, pulsed increases in rodent populations in areas with higher human densities may prompt similar responses in AR application, spilling over to higher AR toxicity among non-target species.

Herein, we explored AR exposure in fishers (*Pekania pennanti*) over a period of 3 years across the heterogeneous region of New York State (NYS), an area spanning mixed agricultural and forested landscapes to wilderness areas within the Adirondack Park. Fishers are generalist

predators and have been documented consuming a wide range of prey items, including seeds, fruits, eggs, insects, carrion, small birds and mammals (McNeil et al. 2017, Kirby et al. 2018, Happe et al. 2021, Smith et al. 2022). While once extirpated from much of the northeastern United States and Canada, populations have rebounded considerably (Lewis et al. 2012) and fishers have proven quite adaptable to disturbed landscapes (LaPoint et al. 2015). In the Northeast, fishers are commonly found in areas previously thought unsuitable, such as suburban forest patches and young, managed forests (Powell et al. 2017 and references therein). Because fishers occupy areas across a gradient of urbanization and development within New York State and are managed for a sustainable harvest that provides annual samples of the standing live fisher population across that gradient, we considered fishers an ideal representative of AR exposure risk in mesocarnivores in the northeast.

Our objective was to identify spatiotemporal drivers in the total number of AR compounds detected within individual fishers, expecting each compound to represent a different exposure event given that each AR product relies on a single active AR ingredient. Further, we investigated the probability of exposure to specific AR compounds to potentially clarify exposure pathways. We developed three overarching hypotheses related to farming, human intrusion into forests, and prey cycles driven by mast seeding, each of which could be represented by various landscape covariates, and included demographic factors such as fisher age and sex that may influence fisher space use and, by extension, AR exposure. For example, we expected sub-adult fishers to have the greatest risk of AR exposure as they disperse from natal territories into unfamiliar landscapes. Overall, we expected that increases in agricultural land cover, intermixing of wildland and urban cover types, and building density would increase the probability of rodenticide exposure in fishers, especially when combined with increased

fragmentation of fisher habitat. We further predicted that years following a high mast crop would see greater AR exposure in fishers due either to 1) lagged increases in small mammal populations and, by extension, increased application of ARs or 2) fishers ranging further in mast failure years to find food and encountering more AR sources along their travels.

## **METHODS**

### ***Study area and sample collection***

Our study was conducted within all areas of New York State (NYS), USA, where sustainable harvests of fishers are managed by the NY State Department of Environmental Conservation (DEC; Figure 1). Land cover was variable across the state, ranging from agricultural-forest matrix in western NYS to the forest-dominated Adirondack Park and Catskill Mountains, with suburban-dominated regions in between. Much of NYS has experienced considerable reforestation in the past 100 years, with old-growth forest almost exclusively restricted to Adirondack Park in northern NYS (Ziegler 2002).

From 2018–2020, fisher carcasses were submitted to the DEC from licensed trappers during the regulated harvest season (Figure 1), which occurs between late October and mid-December, with some regional variability in season length (6, 30, or 46 days). From each carcass, DEC personnel extracted a liver sample and tooth (LPM4); cementum annuli aging was conducted by Matson’s Laboratory (Manhattan, MT). Sex was determined by the presence/absence of a baculum and recorded by trappers on a furbearer possession tag (FPT) for each harvested fisher. Liver tissue was stored in zip-top bags or plastic sample tubes in the freezers at State University of New York College of Environmental Science and Forestry (SUNY ESF) prior to being sent out for rodenticide screening as described below.

From among the larger sample of harvested fishers, we selected samples for this study in a quasi-random manner based on a gradient of forest cover. Precise trapping locations were not recorded, so we used the town, county, and wildlife management unit (WMU) information recorded on the FPT. Because WMU and town boundaries are often arbitrary rather than following roads or natural features, we inspected location information and corrected parts of the record attributes that did not align, i.e., we edited town or WMU if two of the three location attributes matched but not the third, presuming that the third was incorrectly recorded. We first determined the center point of the smallest spatial unit for each harvested fisher (i.e., usually the intersection of town and WMU). Next, we calculated the percentage forest within a 10×10 km grid using 2019 National Land Cover Database data (NLCD; Dewitz and U.S. Geological Survey 2021), broke forest cover into quantiles, and then selected an approximately even number of samples across quantiles, based on the grid cell in which each town/WMU center point fell. While we attempted to further balance samples by age and sex classes, the sample was skewed towards females due to a companion productivity study for which the carcasses were originally collected.

### ***Toxicological screening***

Each liver sample was tested for seven FGARs (warfarin, dicoumarol, coumafuryl, chlorophacinone, coumachlor, diphacinone, pindone) and four SGARs (brodifacoum, bromadiolone, difenacoum, difethialone) at the Pennsylvania Animal Diagnostic Laboratory System in New Bolton, PA following established protocols (Vudathala et al. 2010). Detection limits were 0.010 ppm (brodifacoum, difenacoum), 0.025 ppm (bromadiolone), 0.050 ppm (chlorophacinone, difethialone, diphacinone), or 0.100 ppm (coumachlor, coumafuryl,

dicoumarol, pindone, warfarin). Detections above these amounts but below the quantifiable limits were marked as “trace” and considered positive detections (Gabriel et al. 2012). We note that coumachlor, coumafuryl, dicoumarol, and pindone are not currently registered for use as ARs in the United States. However, dicoumarol can be found naturally in sweet clover hay that has become moldy (Slankard et al. 2019), causing coagulopathy in animals that ingest it (Radostits et al. 1980). Because this compound can be found naturally, we examined it separately.

### *Spatial data*

Because we were unsure of the specific harvest location for each sample, we used a multiple imputation approach to produce missing point locations and account for variability (Murray 2018). Similar methods have been used successfully for imputing missing data in epidemiological (Sterne et al. 2009) and wildlife (Frair et al. 2004, Blanchong et al. 2006) applications. We generated 10 random locations (Schafer 1999) within each combination of town and WMU to represent potential locations for each sample. When generating random points, we removed areas of town/WMU polygons that were classified by NLCD as open water, barren land, wetlands, agriculture (hay/pasture and cultivated crops) because we expected trapping of fishers to be unlikely to potentially impossible in these areas. Matching fisher harvest locations from Jensen and Humphries (2019)—collected between 2005 and 2013—to the 2008 NLCD layer indicated that 84% of fishers harvested in northern New York were in forested areas (with an additional 11% trapped in woody wetlands). Likewise, we removed areas >2 km from a road as trappers are generally arrange their traplines near roads (Hodgman et al. 1994, Wiebe et al. 2013). To characterize spatial drivers of exposure, we first generated circular buffers around

each imputed sample point, with radii based on fisher home range sizes (15 km<sup>2</sup>; Fuller et al., 2016), patterns of resource selection (30 km<sup>2</sup>; Jensen and Humphries, 2019), and a broader landscape context (60 km<sup>2</sup>). Within each buffer, we calculated percent land cover or summarized metrics (e.g., mean, sum) to describe the landscape variable of interest. We extracted the percent of agriculture and forest cover from the 2019 NLCD layer (Dewitz and U.S. Geological Survey 2021). The NLCD layer contains separate land cover classifications for cultivated crops and hay/pasture, as well as for deciduous, evergreen, and mixed forest types. We retained each of these individual land cover types but also combined cultivated crops and hay/pasture into 'total agriculture' and combined deciduous, evergreen, and mixed classes into 'total forest'.

For mastling data, we focused on American beech (*Fagus grandifolia*), one of the dominant and most wide-spread mast crop producers in NY State (Jakubas et al. 2005). Researchers at the SUNY ESF Huntington Wildlife Forest (44°00'N, 74°15'W) near Newcomb, NY have been collecting beech mast data since 1988 (S. McNulty, unpublished data), and we retained their data from 2017 to 2020 to test present year and lagged effects of beech mastling on AR exposure in fishers. Because beech seeds are produced in the fall (i.e., August–October), there is generally a delay before any small mammal populations increase (Jensen et al. 2012). Because fishers are generalist predators, they commonly switch primary prey depending on availability (Bowman et al. 2006). Therefore, we considered several possibilities relating to the relationship between rodenticide exposure in fishers and mast cycles: a) fishers exploit beech nuts as a resource, and therefore may be less likely to be exposed to rodenticide baits or poisoned prey in years with high mast, b) rodenticide use increases in response to greater rodent numbers, which would increase AR exposure in fishers in the year following a mastling event. However, we also expect that the human response (i.e., rodenticide deployment) would vary according to

the size of the mast crop because only the largest crops result in the strong population-level response of small mammals (Jensen et al. 2012). During our study period, 2018 and 2020 were mast failure years, while mast crops were produced in 2017 and 2019 (S. McNulty, unpublished data).

We expected beech mast to have a greater impact where beech trees were more prevalent, and thus extracted beech basal area per acre data from the Forest Inventory and Analysis (FIA; Bechtold and Patterson, 2005) database for NYS using the *rFIA* package (Stanke et al. 2020). To predict beech basal area across NY State, we implemented a random forest algorithm using the *ranger* package (Wright and Ziegler 2017) and a similar suite of covariates as those described in Riley et al. (2016), including the existing vegetation cover, vegetation type, and vegetation height layers from LANDFIRE (Rollins, 2009; available at [www.landfire.gov](http://www.landfire.gov)) and the 30-year (1991–2020) climate normals from PRISM (PRISM Climate Group Oregon State University 2022). The full list of covariates is included in Appendix S1: Table S1. We tuned the model by comparing root mean square error (RMSE) with various parameter values. Ultimately, we predicted beech basal area per acre across the state at a 250-m resolution (Appendix S1: Figure S1) and masked the raster to exclude areas that did not contain deciduous or mixed forest according to the 2019 NLCD (Dewitz and U.S. Geological Survey 2021). We then converted beech basal area per acre to total basal area (m<sup>2</sup>) per 250-m resolution cell.

We examined several metrics to describe human encroachment into fisher habitat. First, we calculated number of buildings within each circular buffer using a raster layer developed from the Microsoft building footprints (Bing Maps Team 2018), counting the number of building centroids that intersected each 250-m cell (Heris et al. 2020). We ultimately converted the number of buildings within a buffer to a 5-level categorical variable (no buildings + quartiles of

building counts). Next, we summarized wildland-urban interface (WUI) data (Carlson et al. 2022), which is based on the density of structures relative to natural vegetation (Bar-Massada et al. 2014; Figure 2). Carlson et al. (2022) used moving windows of various radii to classify pixels into landscapes having  $>6.17$  buildings/km<sup>2</sup> and either  $>50\%$  wildland vegetation (so-called “intermix”, hereafter WUI<sub>im</sub>) or within 2.4 km of large ( $\geq 5$  km<sup>2</sup>) blocks of primarily natural vegetation (so-called “interface”, hereafter WUI<sub>if</sub>). We retained for our analyses the three smallest radii (i.e., 100, 250, and 500 m) for two reasons: 1) the larger radii were unable to capture smaller clusters and individual buildings, which we predicted may be important in determining risk of AR exposure in fishers, and 2) because the differences from one level to the next were smaller once radii size exceeded 500 m (Carlson et al. 2022).

Development and manipulation of spatial layers was performed using a combination of ArcGIS 10.4.1 (ESRI, Redding, CA) and the *sf* (Pebesma 2018), *terra* (Hijmans 2021), and *tidyverse* (Wickham et al. 2019) packages in Program R version 4.2.1 (R Core Team 2023). Values were extracted from raster layers using the *exactextractr* package (Baston 2022).

### ***Statistical analyses***

Because lethal concentrations of ARs can vary widely among compounds, as well as within and among species (Quinn 2019), we considered the dependent variable for AR exposure to be: 1) the total number of compounds detected in a sample (which varied from 0–5) and 2) a binary outcome for four specific AR compounds (brodifacoum, bromadiolone, diphacinone, dicoumarol). We calculated Moran’s I statistic to test for spatial autocorrelation of rodenticide exposure using the *ape* package (Paradis and Schliep 2019). Because the Moran’s I test provided no evidence to support a hypothesis of spatial autocorrelation (Appendix S2: Table S1), we fit



generalized linear mixed effects models. We modeled the number of compounds detected in an individual as a function of spatial covariates via a Conway-Maxwell Poisson distribution with a log link. The Conway-Maxwell Poisson distribution is better able to handle under-dispersed count data than the standard Poisson distribution (Shmueli et al. 2005). We modeled the probability of exposure to a specific compound with logistic regression.

We used a multi-step approach to model development (e.g., LeBeau et al. 2017). We first tested the spatial scale (varying buffer size) for each covariate (Table 1) using the pooled data (i.e., all 10 possible imputations for each sample) and included a random effect for sample ID. We likewise fit preliminary models to determine informative combinations of sex, age, age<sup>2</sup>, and their interactions. We compared models via Akaike's Information Criterion for small samples (AICc) and considered models with  $\Delta\text{AICc} < 2$  to be competitive (Burnham and Anderson, 2002). After selecting for scale (buffer size) and covariate subset (e.g., whether to use cultivated crops, pasture, or total agriculture to represent farming), we fit a set of 9 global models including covariates for our three hypotheses (farming, human encroachment, and prey cycles). The global models reduced uncertainty when  $>1$  scale or covariate was selected from the single-covariate models. Our final step was to estimate regression parameters for each set of imputed locations. We included a random effect for WMU (55 levels) for number of compounds and binary models but used a random effect for region (7 levels) to improve parameter identifiability for the dicoumarol models. We report parameter estimates and 95% confidence intervals (CI) averaged across all 10 imputations and interpreted coefficients to be impactful if the confidence intervals did not contain zero.

Analyses were performed in R version 4.2.3 (R Core Team 2023), and all continuous covariates were centered and scaled prior to model fitting (Schielezeth 2010). Regression models

utilizing the Conway-Maxwell Poisson implemented with the *glmmTMB* package (Brooks et al. 2017). Logistic regression models were implemented using the *lme4* package (Bates et al. 2015). We calculated AICc via the *MuMIn* package (Barton 2020). We used the *performance* package (Lüdecke et al. 2021) to calculate variance inflation factors for assessing multicollinearity and to calculate conditional and marginal  $R^2$  values (Nakagawa and Schielzeth 2013). We assessed model predictive capacity using 5-fold cross-validation.

## RESULTS

We screened 100 samples/year in 2018 and 2019 and 138 samples in 2020. In total we tested 338 fishers for AR residue, a sample that included 112 males and 226 females from 0.5–8.5 years old (assuming all fishers were born 1 April each year). Geographically, these samples represented 211 unique combinations of town and WMU. We detected anticoagulant rodenticides in 282 (83%) of tested livers (Table 2). We detected fisher exposure to eight different compounds (brodifacoum, bromadiolone, chlorophacinone, dicoumarol, difenacoum, difethialone, diphacinone, warfarin). Coumachlor, coumafuryl, and pindone were not detected in any sample. Overall, diphacinone was the most-detected compound ( $n = 249$  fishers tested positive; 74%), followed by brodifacoum ( $n = 196$ ; 58%) and bromadiolone ( $n = 101$ ; 30%). Chlorophacinone, difenacoum, and warfarin were detected only in trace amounts (and in <10 individuals). The maximum number of compounds detected per individual was five ( $n = 2$ ), while most individuals (79%) tested positive for one ( $n = 78$ ), two ( $n = 120$ ), or three compounds ( $n = 69$ ).

### *Covariate selection for parameter estimation*

Our main focus was investigating hypotheses related to three main drivers of anticoagulant rodenticide exposure: farming and agricultural activities, small mammal populations due to mast cycles, and encroachment of humans into forest habitats. In the individual models, total WUI and  $WUI_{im}$  were competitive in the WUI set, but otherwise only one scale was selected for each covariate group (i.e., pasture instead of crops or total agriculture, building categories instead of total number of buildings, and deciduous forest instead of evergreen or mixed forest. All variables were selected at the 15 km<sup>2</sup> buffer, except for total WUI, which was competitive in a 30 km<sup>2</sup> buffer. We examined a set of 9 global models incorporating covariates to address each of the hypotheses (Table 3). There were two models in the global set with  $\Delta AICc < 2$ , so we choose the most parsimonious model to investigate drivers of AR exposure. We estimated parameters for the effects of sex, age ( $x + x^2$ ),  $WUI_{im}$  (100 m window), pasture, beechnut count in the previous year, beech basal area, and an interaction between lagged beechnut count and beech basal area. We note that the second-best global model (with a weight of 0.30, Table 3) included an interaction between percentage of deciduous forest and building counts (quantiles) instead of  $WUI_{im}$ , as well as a binary indicator for mast seeding or failure year instead of beechnut production.

We used the same suite of covariates to investigate the probability of exposure to brodifacoum, bromadiolone, and diphacinone, but we could not test the full set for dicoumarol, likely due to low frequency of exposure. However, we were specifically interested in the potential relationship between dicoumarol exposure and livestock farms that might have sweet clover hay, so for this compound modeled the effects of sex, age ( $x + x^2$ ), and pasture.

### ***Expected number of compounds***

Age and sex were the strongest predictors of the number of AR compounds detected in a fisher liver (Appendix S2: Table S2). The number of compounds detected was greater in males (predicted  $\bar{x} = 2.1$ , 1.9–2.4 95% CI) than females ( $\bar{x} = 1.8$ , 1.6–2.0 95% CI) and increased with fishers age up to 3.9 years but declined in fishers 4 years and older (Figure 3a). As the proportion of area surrounding a location (15 km<sup>2</sup> buffer) increased in WUI<sub>im</sub>, so too increased the number of AR compounds detected within fisher livers (Figure 3b). We observed a slight trend for the lagged masting index effect on the number of compounds detected, with increased beechnut counts related to increased number of expected compounds (Figure 3c), although the coefficient estimate was not significantly different from zero (Appendix S2: Table S2). The proportion of pasture area also did not influence the number of AR compounds detected (Figure 3d). The proportion of variance explained by the entire model was 0.14 (conditional R<sup>2</sup>), and the proportion of variance explained by only the fixed effects was 0.12 (marginal R<sup>2</sup>). The results of the 5-fold cross validation indicated moderate to high accuracy (e.g., 0.53 to 0.99) for each number of compounds. However, the balanced accuracy, which accounts for imbalanced classes, ranged from 0.50–0.59 for 0–5 compounds (Appendix S2: Table S3). This indicates that our model had only moderate success in predicting the number of compounds by our selected covariates.

### ***Probability of exposure to individual compounds***

Consistent with predictions for the number of different compounds a fisher was exposed to, age generally had the strongest effects on predicted probability of AR exposure for any single compound (Figure 4; Appendix S2: Table S3). Across all three compounds, the probability of

exposure to a specific compound peaked in fishers between 3.6 to 4.5 years old. Likewise, males generally had higher probabilities of exposure (Figure 4), but the difference was only significant for diphacinone, where the odds of exposure for males were increased by 2.1 (1.1–3.8 95% CI).

Here again, the proportion of area around a sample location classified as  $WUI_{im}$  explained substantial variation in the predicted probability of exposure to brodifacoum and bromadiolone (Figure 5). The effect size was similar among compounds, increasing the odds of exposure by 1.4 on average with each increase of 0.06%  $WUI_{im}$  within the 15 km<sup>2</sup> buffer. The effect of  $WUI_{im}$  on exposure to diphacinone was not significant but trended positive (Figure 5). The lagged masting index explained variation in probability of exposure only to bromadiolone, with odds of exposure increasing by 1.4 (1.1–1.8 95% CI) with each increase of 120 beechnuts in the previous years' count (Figure 6). Pasture was not a significant predictor of probability of exposure to brodifacoum, bromadiolone, diphacinone, or dicoumarol (Figure 7), nor was the interaction between beechnut count and beech basal area (Appendix S2: Table S3). The conditional and marginal  $R^2$  values were similar for brodifacoum (0.14 conditional, 0.12 marginal), bromadiolone (0.25 conditional, 0.21 marginal), diphacinone (0.19 conditional, 0.16 marginal) and dicoumarol (0.09 conditional, 0.08 marginal), suggesting that spatial unit random effects did not explain considerably more variation than the fixed effects.

## **DISCUSSION**

Anticoagulant rodenticide exposure is a persistent threat to carnivores and scavengers (Elliott et al. 2016), so we used samples from harvested fishers to investigate the extent of rodenticide exposure across New York State. This analysis was motivated by observations from a related telemetry study in rural parts of northern NYS, including the Adirondack Park, where several

mortalities of fishers that appeared otherwise healthy were attributed to rodenticide (S. Cunningham, unpublished data). Prior to those observations, rodenticide exposure was not on our radar for fishers since illegal cannabis cultivation—one of the primary sources of AR exposure in California fishers—in the region is negligible compared to west coast states (Koch et al. 2016). Nevertheless, our results add to the growing body of literature demonstrating that anticoagulant rodenticides are ubiquitous across the landscape, even within largely forested landscapes, with dwellings and other structures intermixed within wildland vegetation being a primary contamination source. The Northeast is experiencing a continuously expanding urban footprint (Shifley et al. 2014), with nearly one third of the region consisting of housing units or other developments intermixed within wildland vegetation (Carlson et al. 2022), and with individual states having >80% of total land cover in WUI (e.g., New Hampshire; Radeloff et al. 2005)—meaning there is a high degree of households and people interacting routinely with wild carnivores. NYS has only 26% WUI, which is driven largely by intermix (18%). However, the Adirondack Park is a mosaic of private and public lands, and seasonal and year-round homes abound across the region (Kretser et al. 2008), as is the case in other heavily forested regions such as the Catskill Mountains (Hagani et al. 2021). Several other studies have demonstrated a link between human population density and AR exposure (Lohr 2018, Pay et al. 2021); therefore, despite it not being on our radar it is no surprise that we observed high rates of AR exposure in NY fisher.

The majority of fishers sampled (83%) showed evidence of rodenticide poisoning, and nearly three quarters of these tested positive for more than one compound. This is important to note because each rodenticide product contains a single AR compound, and therefore the presence of multiple compounds indicates multiple exposure events. Brodifacoum,

bromadiolone, and diphacinone dominated AR exposure in fishers in our study and also have been frequently detected in raptors across the Northeast (Murray 2017). Given the availability of diphacinone-containing products available to general consumers (U.S. Environmental Protection Agency 2008), we expected exposure to this compound would be driven largely by  $WUI_{im}$  (i.e., intermix). AR exposure tended to increase with increasing  $WUI_{im}$ , although the effect size was not large. We also considered that  $WUI_{im}$  may not capture the full effects, as the weight for the model including building counts was high as well, though because both  $WUI_{im}$  and the interaction between forest cover and building counts were selected to quantify encroachment of humans into forest habitats, we interpreted them as supporting the same hypotheses. We were surprised that probability of exposure to brodifacoum and bromadiolone was more strongly predicted by intermix, although we note from personal observations that several SGARS are available on the shelves of farm supply stores. Although the amounts on the shelves followed EPA restrictions, private citizens frequently use more rodenticide than necessary and often do not read, let alone follow, instructions on the packaging (Bartos et al. 2012). Thus, we surmise that SGARs are purchased and distributed indiscriminately beyond agricultural settings.

Our data indicate that behavioral differences between fisher age and sex classes may contribute to differential probability of rodenticide exposure. We originally hypothesized that subadult (i.e., 1.5–2.5 years old) animals would exhibit the greatest number of compounds and probability of exposure because these animals are dispersing from natal ranges and establishing their own territories (Matthews et al. 2013). However, the peak number of compounds and highest probability of exposure were generally observed in fishers 3.5–4.5 years old, likely past the point of territory establishment and overlapping prime breeding years. Previous work examining AR exposure in mink (*Neovison vison*) showed an increasing number of compounds

in mink from 0 to 5 years of age, which the authors attributed to the long retention of SGAR compounds in liver tissue (Ruiz-Suárez et al. 2016). We expect that this is likely also the case in fishers and speculate that the lower exposure in older age classes that we observed could be due to smaller sample sizes of older animals, or dominant animals occupying areas with little human encroachment (which may have also contributed to greater age at harvest). The expected number of compounds and probability of exposure to diphacinone were also greater in males than females. Although diets are expected to be similar between sexes, male fishers are substantially larger than females and require greater food intake on a regular basis (Giuliano et al. 1989, Smith et al. 2022). Yet, lactating females require a much greater energy intake (Powell and Leonard 1983), and therefore at certain times of the year could be experiencing prey intake rates similar to males. Male fishers also use substantially larger home ranges than females (Zielinski et al. 2004, Weir et al. 2009), and range even further during the breeding period to where home ranges cannot be defined (Kordosky et al. 2021). Perhaps this difference in space use, rather than energetic requirements, may be driving sex-based differences in AR exposure.

Lagged effects of beech masting explained some variation in overall number of compounds a fisher was exposed to as well as the probability of exposure to bromadiolone, although the effects were not as strong as we anticipated. Importantly, beech trees are not the only mast-producing species in the northeast and not all tree species have synchronized masting cycles (Schnurr et al. 2002). Consequently, our detection of any effect bears further consideration. The lack of effects on probability of exposure to diphacinone was surprising, as we expected the lagged beechnut count to act as a proxy for increased rodent populations the following year, and for that increase to spur homeowners to more expansive use of rodenticides. Diphacinone should be the mostly widely accessible compound for homeowners. Probability of



exposure to bromadiolone, one of the compounds favored by pest management professionals (Memmott et al. 2017, Murray 2017), did increase with the lagged masting index. Pest management professionals may be hired by individuals or businesses to control a range of pests, rodents included, so we speculate that large rodent outbreaks may trigger a call to a professional instead of home or business owners attempting to handle it themselves. However, as noted previously, bromadiolone products are sold off the shelf in farm stores, so also may be accessible for private rather than professional deployment. The effects we detected, while minor, justify further consideration of masting cycles and other ecological drivers of small mammal populations and the use of rodenticides to contain them, especially as climate change is expected to increase small mammal populations in the region (Stenseth et al. 2003, Murray 2017) as well as the number and variability in mast seeding events (Allen et al. 2014). The number of beech nuts recorded in 2019 was exceptionally high (S. McNulty, unpublished data), and therefore we consider the possibility of observing stronger effects of masting events on AR exposure in the future.

Pasture was not an important driver of rodenticide exposure for fishers across NYS. However, the areas of most intensive agriculture in New York (i.e., Eastern Great Lakes Lowlands south of Lake Ontario) were closed to fisher harvest during this study, and the lack of fisher samples from this region could certainly influence our ability to detect agriculturally related exposure risks, in which case the 83% of fishers that tested positive for rodenticide would be biased low. We did detect exposure to dicoumarol, which requires mold to form on hay (Radostits et al. 1980) since dicoumarol has not been a marketable AR compound for several decades. While we could not identify which areas of pasture were used for livestock farming, we assumed a large portion of pastureland was associated with dairy farming, a declining but still

major agricultural sector across New York (Winsten et al. 2010). The lack of AR exposure from agriculture that we observed could be due to general fisher avoidance of large open areas (Spencer et al. 2011, Thompson et al. 2011), combined with AR instructions to place baits close (i.e., within 15 m of buildings) to buildings. Therefore, even if rodent control activities are present in dairy operations, bait distance restrictions may limit the availability of poisoned prey for fishers. The pattern of agriculturally driven AR exposure may be more prominent in species that are more likely to use agricultural areas for travel or hunting, such as red foxes (*Vulpes vulpes*; Tosh et al. 2011a) or mink (Ruiz-Suárez et al. 2016), or raptors that depend on open areas to hunt ground-dwelling rodents or prey on highly mobile passerines (Hughes et al. 2013).

Using harvested fishers presents several challenges for investigating AR exposure, but also provided benefits not found in many previous studies on rodenticide exposure. Samples from harvested animals provide researchers with vast numbers of samples across time and space that would be otherwise unobtainable (Heffelfinger et al. 2013, White et al. 2015), and in studies of AR exposure, provide a sample that is potentially less biased than opportunistic collections of dead animals having already succumbed to the effects of AR toxicity (Ruiz-Suárez et al. 2016). We were unable to determine if fisher had ingested acutely lethal dosages, or if poisoned animals were affected in such a way that they became more vulnerable to being trapped (e.g., if coagulopathy resulted in impaired ability to hunt, thus increasing susceptibility to baited traps). Previous work in Denmark revealed declining body condition due to ARs in weasels and stoats (*Mustela erminea*; Elmeros et al. 2011), evidence for an “impaired condition hypothesis” that suggests greater vulnerability to injury, disease, extreme weather, and other toxicants (Rattner et al. 2014). Similarly, common kestrel (*Falco tinnunculus*) nestlings had lower body weight in agricultural areas treated with bromadiolone (Martínez-Padilla et al. 2017). Although SGAR

residues persist in the liver tissue for extended periods of time (Vandenbroucke et al. 2008), harvest is limited to a few short weeks in late fall that may limit insights to a short window of time, masking seasonal differences in exposure. This is likely true especially for FGARs because retention of these compounds in the liver is often considerably shorter than SGARs (Horak et al. 2018). Indeed, it is difficult to interpret the concentration of residues, as the initial dose and timing of ingestion is unknown (Murray 2020, Rattner and Harvey 2021), and trace detections or low concentrations could indicate that either the AR was ingested several months prior or more recently but in very small amounts. Toxicity could lead to death prior to the trapping season, masking the full scope of effects (e.g., acute toxicity in pregnant or lactating females or their offspring). Another challenge was that we were unable to obtain a precise spatial location for each sample, and may have introduced excessive variation into potential spatial effects by having iteratively imputed potential sample locations within a large township. We are confident that our imputation process did not introduce bias as we carefully eliminated areas within each spatial unit where fishers were unlikely to be harvested, such as cultivated crop fields or urban areas, therefore reducing potentially erroneous locations. Furthermore, we examined the distribution of covariate values across imputations and observed a high rate of similarity in distributions among iterations (Appendix S3: Figure S1). We thus attribute the general low predictive ability of our models to the ubiquity of rodenticide across the landscape.

An important aspect of managing rodenticide exposure is considering the patterns and psychology of AR use by individuals and pest management professionals. A survey of farmers in Northern Ireland revealed that adherence to best practices for reducing secondary exposure is variable and infrequent (Tosh et al. 2011b), and we assume that this is likely the case in North America as well. California pest management professionals expressed concern over the use of

rodenticides by the general public (Steinberg et al. 2015), but even professional applicators have shown inattention to best practices (Memcott et al. 2017). In NYS, it is unknown how many or how often homeowners apply rodenticide products to their property, or the triggers that prompt use of rodenticide instead of traps. Proper application of rodenticide compounds could go a long way to reducing the impacts of secondary exposure (Tosh et al. 2011b, Memcott et al. 2017), and snap traps could reduce risk even further. Changes in human behavior will likely only be achieved through education on rodent behavior, how rodenticides work, risks of secondary exposure, and the consequences of improper use (U.S. Environmental Protection Agency 2008, Memcott et al. 2017). And for that, fishers may not be the ideal representative compared to a more charismatic species, for example, bobcats (Serieys 2014), yet the widespread distribution of both fishers and fisher trappers in the northeastern United States means fishers provide a greater number and more reliable sample for testing AR exposure than do rarer and more geographically constrained bobcats in the region. Ultimately, multiple species should be compared given different behavioral tolerances for areas dominated by humans and differential habitat use patterns (Lesmeister et al. 2015) that likely affect exposure levels.

One of the greatest challenges in accounting for AR effects is the disconnect between wildlife managers and pesticide managers. The regulatory bodies that manage rodenticide registration and use (e.g., EPA; Witmer and Eisemann 2007) are often separate from wildlife management agencies, and there appears to be little enforcement of proper AR use (Quinn et al. 2019). Yet very few studies have investigated the population-level impacts of rodenticide exposure (Rattner et al. 2014), or the sub-lethal effects of chronic exposure (Lohr 2018), despite the ever-growing and global evidence of high exposure rates in non-target wildlife. Without demonstration of population-level effects, it is difficult for wildlife managers react to AR risk.

Yet given the nature of AR exposure, it may be logistically or financially infeasible to study population-level impacts. Meanwhile, there have been some indications that exposure of wildlife to SGARs has increased in the past two decades (Coeurdassier et al. 2019, Rattner and Harvey 2021), and is projected to increase into the future. Therefore, investigating the ecological and social factors that drive exposure may be the best way forward to understand exposure risk and subsequent consequences for wildlife management.

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## TABLES

Table 1: Hypotheses and covariates related to anticoagulant exposure in fishers across New York State (2018–2020) that were tested for scale, at buffer sizes of 15, 30, and 60 km<sup>2</sup>.

<b>Hypothesis Covariate</b>	<b>Description</b>
<i>Farming</i>	
Agriculture land cover	Percent of land cover classified as agriculture within the buffer. Measured as pasture-only, crops-only, and combined total agriculture
<i>Human encroachment</i>	
Continuous building count	Summed number of buildings calculated from building raster
Categorical building count	Number of buildings grouped into four categories for quartiles, and an additional category for 0 buildings
Wildland-urban interface	Percent of land cover classified as wildland-urban interface (WUI). Measured as intermix-only, interface-only, and total WUI
Buildings × forest	Investigating the role of building density across the gradient of forest cover
<i>Mast-driven prey dynamics</i>	
Beechnut count	Annual count of beechnuts from Huntington Wildlife Forest in northern New York. Included for each year $t$ and $t-1$
Categorical mast/failure	Binary indicator for mast (2019) and mast failure years (2018 and 2020)
Beech basal area	Summed beech basal area (m <sup>2</sup> ) within a buffer
Basal area × beechnut interaction	Investigating the potential change in impact of interannual differences related to beech mast across space

**Table 2:** Number of AR detections in harvested fishers in New York State, 2018–2020, divided into groups based on measurable amounts of rodenticide, trace detections, and number of fishers in which each compound was not detected. We tested for 11 compounds but three (pindone, coumafuryl, and coumachlor) were not detected in any sample.

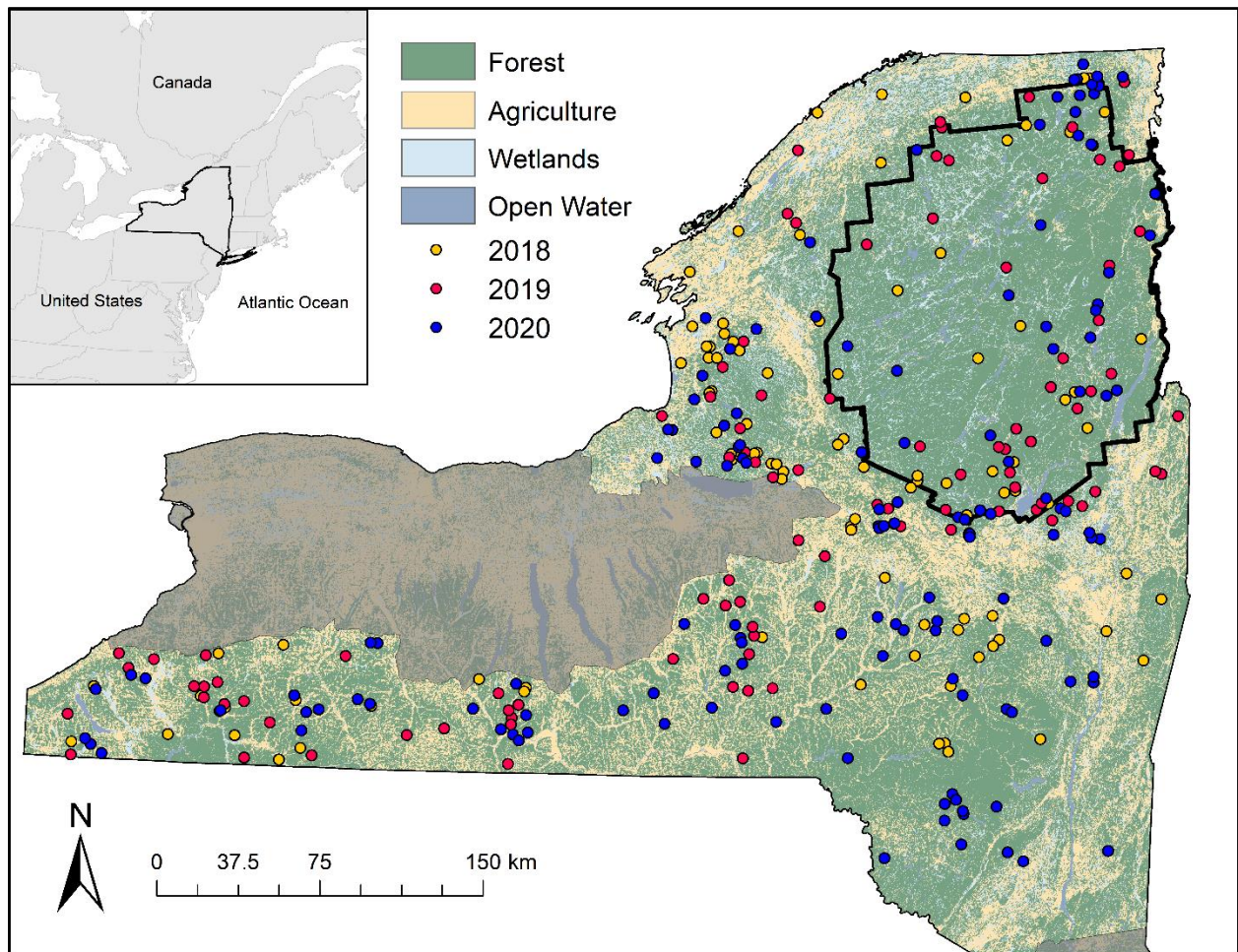
Compound	Type	Quantifiable detections	Trace detections	Not detected
Brodifacoum	SGAR	124 (37%)	72 (21%)	142
Bromadiolone	SGAR	61 (18%)	40 (12%)	237
Chlorophacinone	FGAR	0	8 (2%)	330
Dicoumarol	FGAR <sup>a</sup>	4 (1%)	19 (6%)	315
Difenacoum	SGAR	0	3 (<1%)	335
Difethialone	SGAR	4 (1%)	8 (2%)	326
Diphacinone	FGAR	105 (31%)	144 (43%)	89
Warfarin	FGAR	0	2 (<1%)	336

<sup>a</sup>Dicoumarol can occur naturally in moldy sweet clover hay.

**Table 3:** Global models to explain variation in the number of anticoagulant rodenticide compounds in fishers. Table shows number of parameters ( $k$ ), Akaike’s Information Criterion for small samples (AICc), difference from the top model ( $\Delta$ AICc), and model weight ( $w$ ). Models included covariates for the proportion of 15 km<sup>2</sup> buffers as total wildland-urban interface (WUI<sub>t</sub>), wildland-urban intermix (WUI<sub>m</sub>), pasture, and deciduous forest; the total beech basal area (BBA) within a 15 km<sup>2</sup> buffer, and number of buildings grouped by quartiles (building<sub>q</sub>). For each set of spatial covariates, we include compared the effects of beechnut count (beech<sub>t</sub>), beechnut count in the previous year (beech<sub>t-1</sub>), and a binary indicator for mast years (mast). All models included a random effect of sample ID.

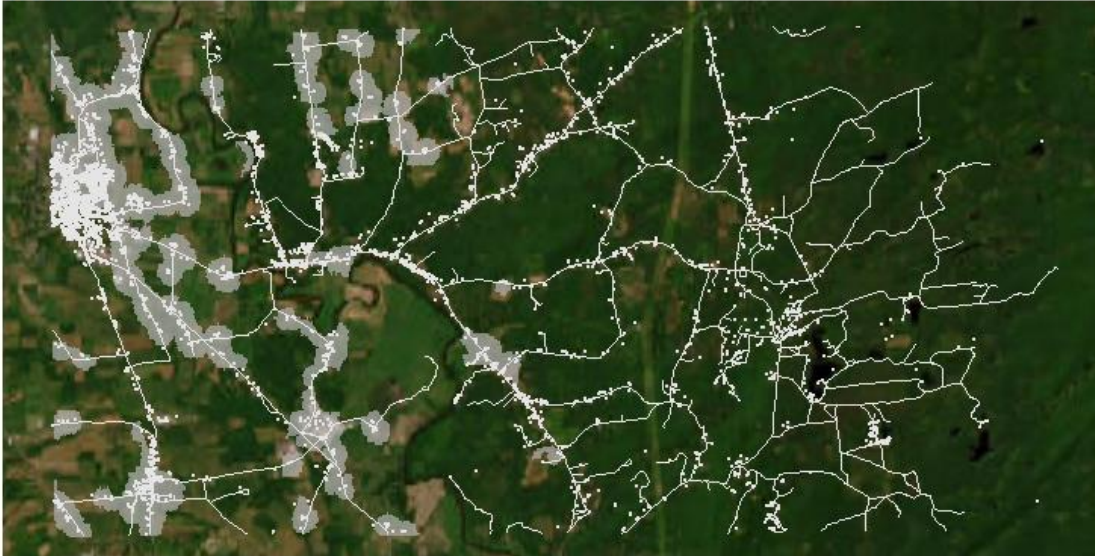
<b>Model</b>	<b><math>k</math></b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>w</math></b>
Sex + Age + Age <sup>2</sup> + WUI <sub>m</sub> + pasture + BBA × beech <sub>t-1</sub>	11	2728.5	0.0	0.39
Sex + Age + Age <sup>2</sup> + building <sub>q</sub> × deciduous + pasture + mast	17	2729.0	0.5	0.30
Sex + Age + Age <sup>2</sup> + WUI <sub>t</sub> + pasture + BBA × mast	11	2760.7	32.2	0.00
Sex + Age + Age <sup>2</sup> + WUI <sub>m</sub> + pasture + BBA × mast	11	2764.9	36.4	0.00
Sex + Age + Age <sup>2</sup> + WUI <sub>m</sub> + pasture + BBA × beech <sub>t</sub>	11	2768.4	39.9	0.00
Sex + Age + Age <sup>2</sup> + WUI <sub>t</sub> + pasture + BBA × beech <sub>t-1</sub>	11	2769.6	41.1	0.00
Sex + Age + Age <sup>2</sup> + WUI <sub>t</sub> + pasture + BBA × beech <sub>t</sub>	11	2773.1	44.6	0.00
Sex + Age + Age <sup>2</sup> + building <sub>q</sub> × deciduous + pasture + beech <sub>t</sub>	17	2776.1	47.6	0.00
Sex + Age + Age <sup>2</sup> + building <sub>q</sub> × deciduous + pasture + beech <sub>t-1</sub>	17	2777.4	48.9	0.00

## FIGURES



**Figure 1:** Map of New York and single iteration of random points for potential sample locations 2018–2020. Greyed-out section is closed to fisher harvest. Bold black outline delineates the Adirondack Park. Point color denotes year of harvest. Inset shows location of New York in the northeastern United States.

Interface

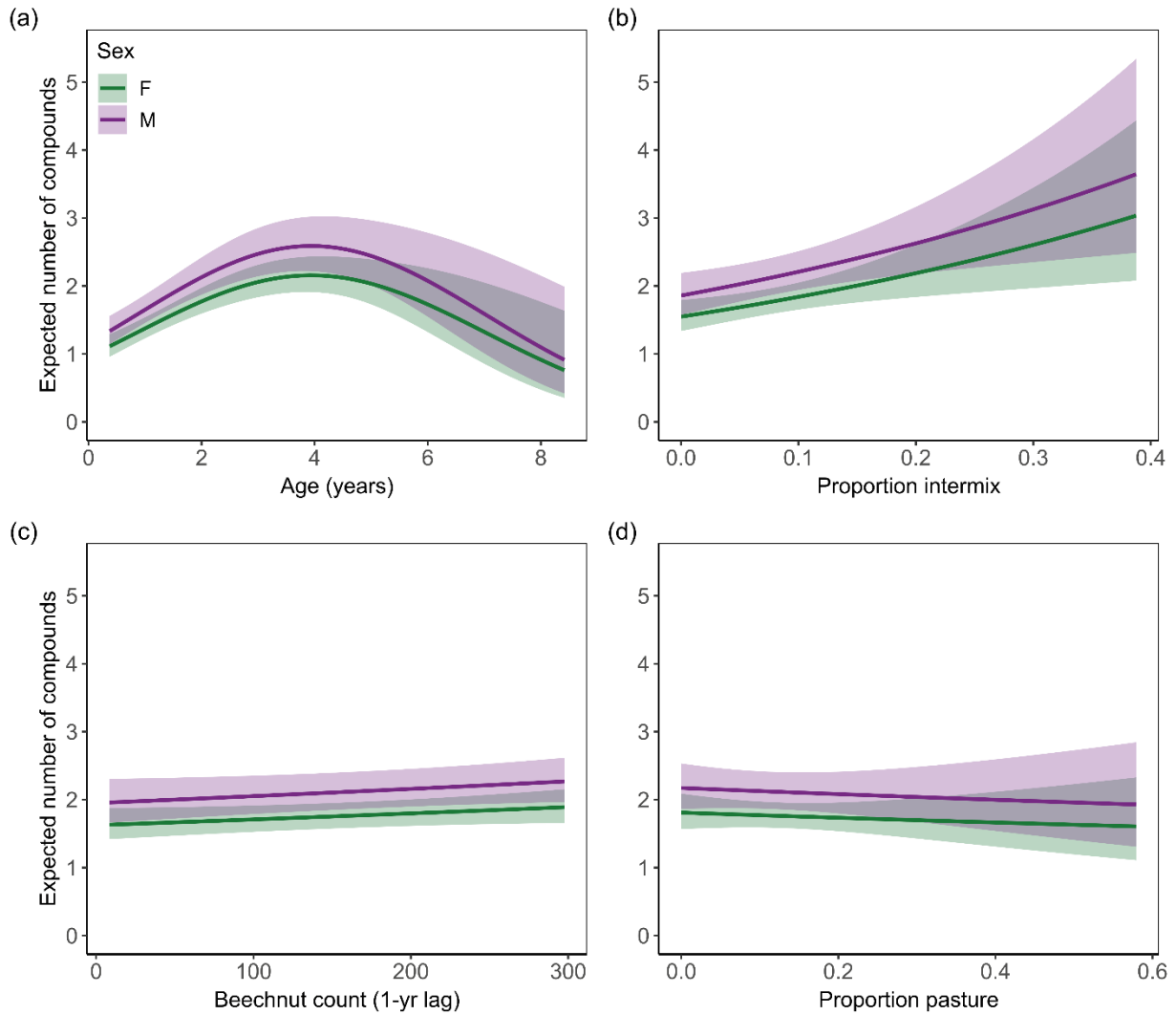


Intermix

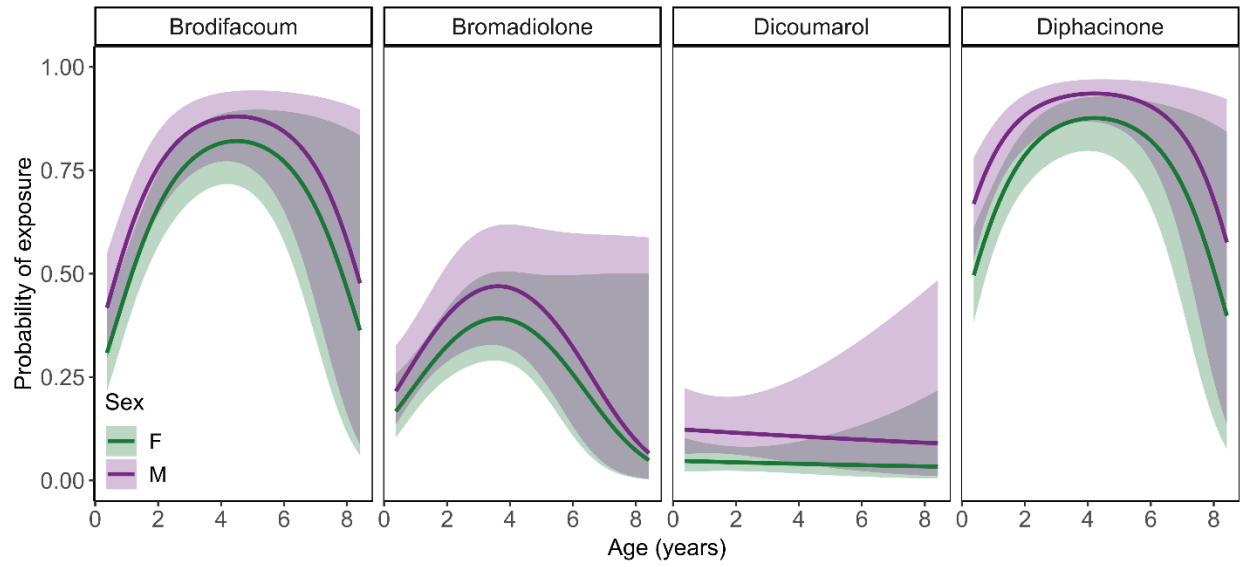


**Figure 2:** Sample contextual landscape showing differences between classification of wildland-urban interface (top; gray areas) versus intermix (bottom). Areas classified as not WUI (i.e., not shaded in either image) are either strictly urban or natural vegetation. Individual buildings are shown as white points, roads as white lines. Darker green in the background is indicative of tree cover, while lighter green and browns tend to be fields, grass, or shrubs. The urban cluster in the upper left corner of each image is the village of Lowville, NY ( $43^{\circ}47'12''\text{N}$ ,  $75^{\circ}29'32''\text{W}$ ). Satellite data from Google Earth.



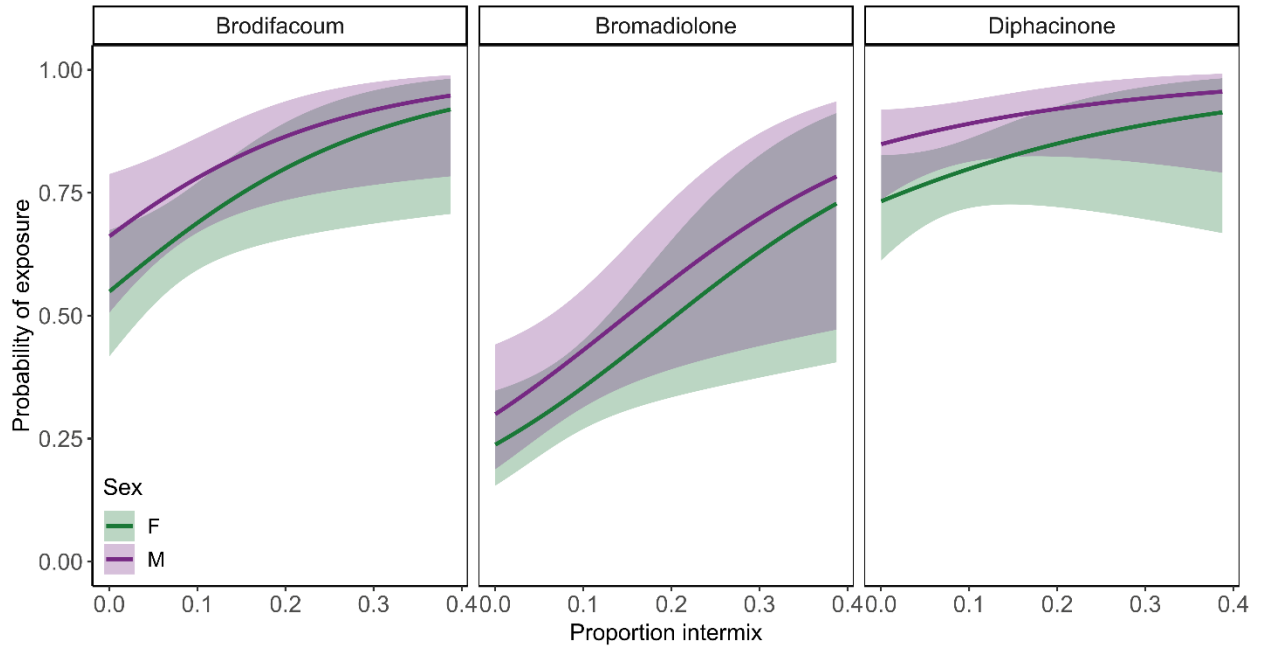


**Figure 3:** Predicted number of rodenticide compounds (from the top model), with 95% confidence intervals, shown separately for male (purple) and female (green) fishers. Plots show effects of fisher age in years (a), proportion of 15 km<sup>2</sup> buffer classified as wildland-urban intermix (WUI<sub>m</sub>; b), number of beechnuts counted during the previous year at the SUNY ESF Huntington Wildlife Forest (c), and proportion of 15 km<sup>2</sup> buffer classified as pasture (d).

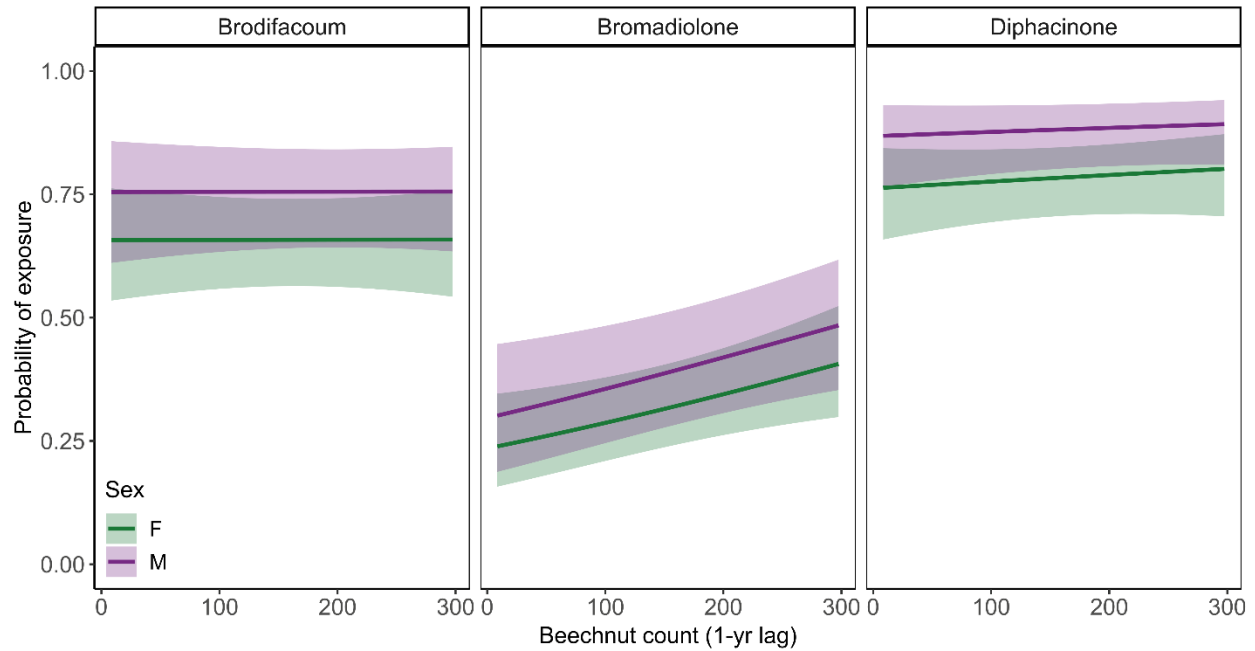


**Figure 4:** Predicted probability and 95% confidence intervals of rodenticide exposure in fishers according to age, and grouped by sex and compound.

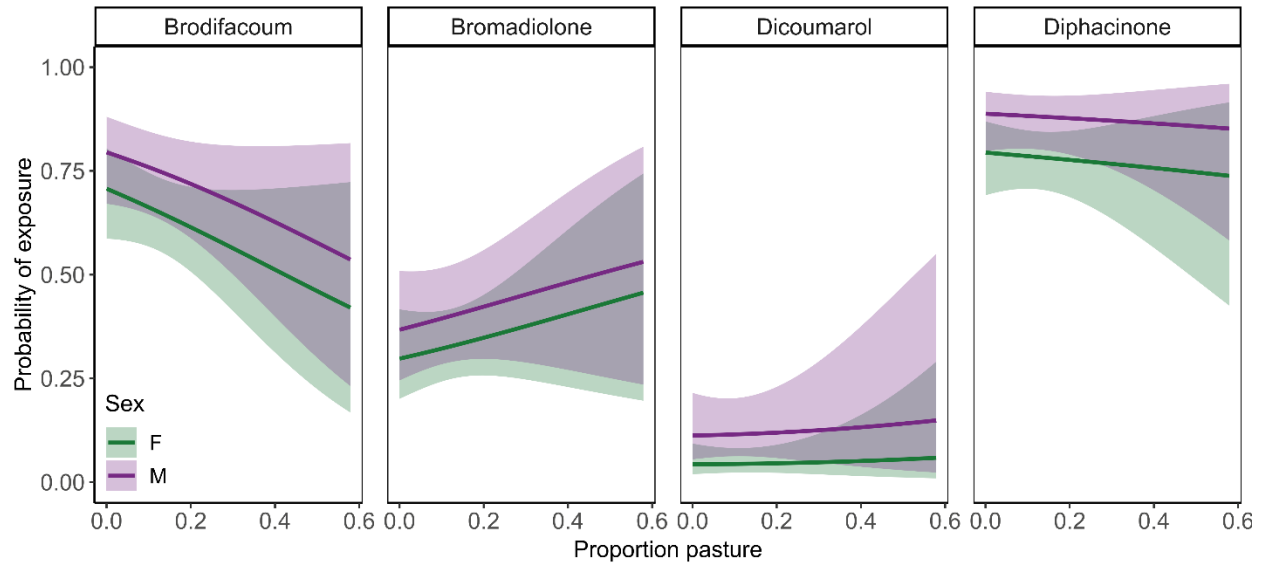




**Figure 5:** Predicted probability and 95% confidence intervals of rodenticide exposure in fishers according percentage of a 15 km<sup>2</sup> buffer classified as wildland-urban intermix, grouped by compound and sex.



**Figure 6:** Predicted probability and 95% confidence intervals of rodenticide exposure in fishers according to number of beechnuts indexed at the SUNY ESF Huntington Wildlife Forest (Newcomb, NY) in the previous year, grouped by compound.



**Figure 7:** Predicted probability and 95% confidence intervals of rodenticide exposure in fishers according percentage of a 15 km<sup>2</sup> buffer classified as pasture, grouped by compound and sex.

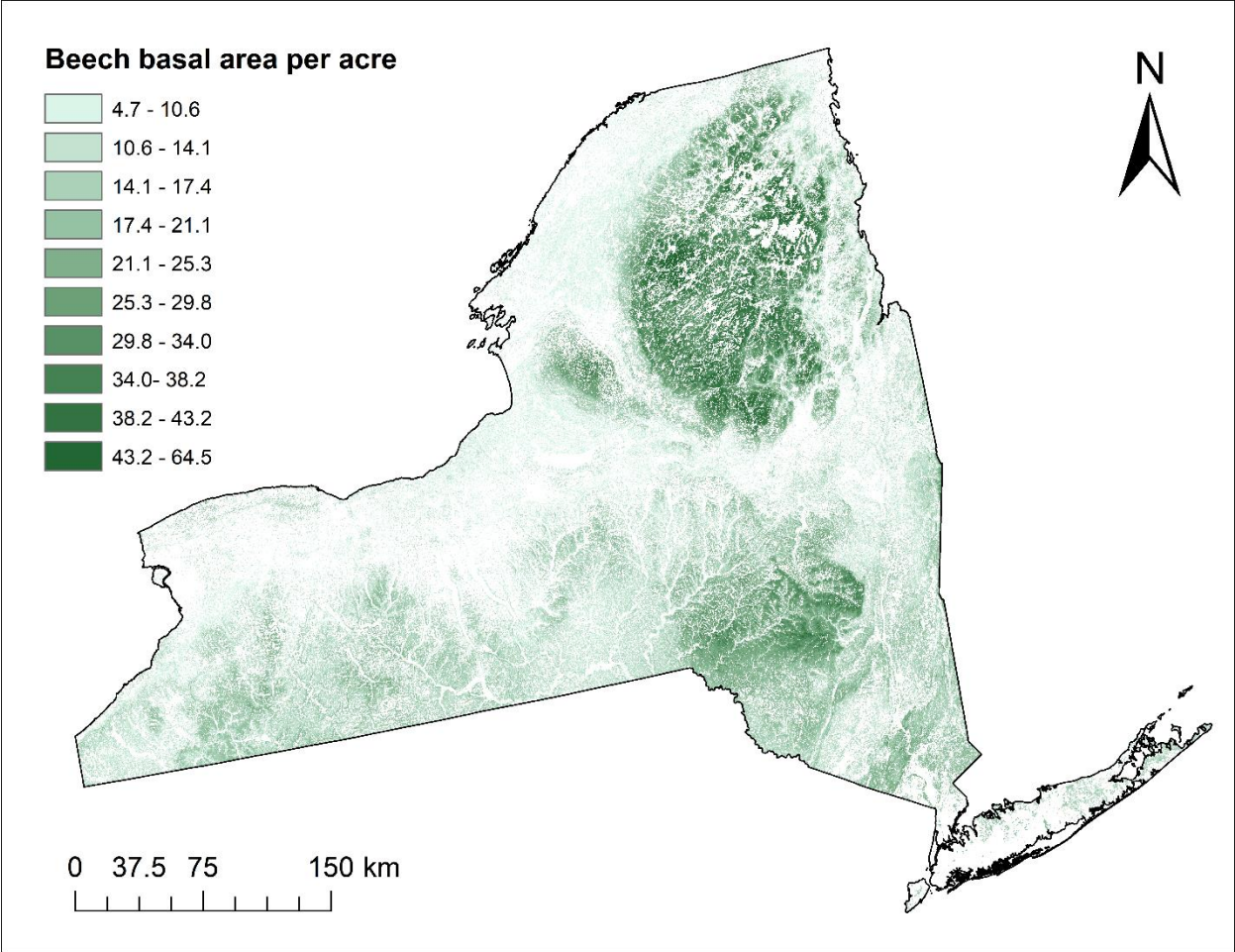
**Appendix 3-1: Development of Random Forest model for predicting American beech (*Fagus grandifolia*) across New York State**

**Table S1.** Full suite of covariates used in developing beech basal area prediction layer, based on Riley et al., 2016. Layers were resampled to align resolution to 250 m.

<b>Layer</b>	<b>Resolution</b>	<b>Source*</b>
Existing Vegetation Cover	250 m	LANDFIRE
Existing Vegetation Type	250 m	LANDFIRE
Existing Vegetation Height	250 m	LANDFIRE
Minimum temperature	935.4 m	PRISM
Maximum temperature	935.4 m	PRISM
Relative humidity <sup>1</sup>	935.4 m	PRISM
Precipitation	935.4 m	PRISM
Solar radiation	935.4 m	PRISM
Vapor pressure deficit <sup>2</sup>	935.4 m	PRISM
Slope	30 m	LANDFIRE
Aspect	30 m	LANDFIRE
Elevation	30 m	LANDFIRE

<sup>1</sup>Relative humidity was calculated from dewpoint and mean temperature

<sup>2</sup>Vapor pressure deficit was calculated as the average of the minimum and maximum vapor pressure deficit



**Figure S1.** Predicted beech basal area (ft<sup>2</sup>) per acre based on Forest Inventory and Analysis (FIA) data, developed with a random forest model.

### Appendix 3-2: Full results from regression models and cross-validation results

**Table A1.** Results of Moran's I test for spatial autocorrelation for number of compounds and binary rodenticide exposure. (mean of 10 imputations)

<b>Model</b>	<b>Observed</b>	<b>Expected</b>	<b>Std. Dev.</b>	<b>P-value</b>
N compounds	0.003	-0.003	0.010	0.573
Brodifacoum	0.005	-0.003	0.010	0.517
Bromadiolone	0.015	-0.003	0.010	0.105
Diphacinone	-0.008	-0.003	0.010	0.476
Dicoumarol	0.009	-0.003	0.010	0.391

**Table A4.** Averaged regression coefficients from 10 random point locations in explaining number of compounds in an individual. Bolded coefficients were interpreted as statistically significant.

	<b>Mean</b>	<b>Standard Error</b>	<b>Z-score</b>	<b>2.5%</b>	<b>97.5%</b>
Intercept	0.5690	0.003	10.50	0.5640	0.5750
<b>Sex (M)</b>	<b>0.1830</b>	<b>0.005</b>	<b>2.520</b>	<b>0.1750</b>	<b>0.1910</b>
<b>Age</b>	<b>0.3280</b>	<b>0.002</b>	<b>6.800</b>	<b>0.3230</b>	<b>0.3330</b>
<b>Age<sup>2</sup></b>	<b>-0.1350</b>	<b>0.001</b>	<b>-4.230</b>	<b>-0.1380</b>	<b>-0.1310</b>
<b>Intermix (15 km<sup>2</sup>, 100 m)</b>	<b>0.1010</b>	<b>0.002</b>	<b>2.840</b>	<b>0.0972</b>	<b>0.1060</b>
Pasture (15 km <sup>2</sup> )	-0.0231	0.003	-0.525	-0.0285	-0.0178
Beech basal area (15 km <sup>2</sup> )	0.0413	0.002	0.958	0.0364	0.0462
Lagged beechnuts	0.0613	0.001	1.740	0.0576	0.0651
Basal area × beechnuts	-0.0902	0.002	-0.265	-0.0133	-0.0048

Variance of random effect (WMU): 0.01

**Table A3.** Accuracy of final Poisson regression model in predicting number of compounds in a fisher liver determined via 5-fold cross-validation. We present each imputed data set separately as well as the overall average.

	Number of compounds detected					
	0	1	2	3	4	5
Imputation 1	0.82	0.60	0.56	0.80	0.97	0.99
Imputation 2	0.82	0.58	0.54	0.80	0.97	0.99
Imputation 3	0.82	0.62	0.55	0.80	0.97	0.99
Imputation 4	0.82	0.58	0.53	0.81	0.97	0.99
Imputation 5	0.82	0.60	0.55	0.79	0.97	0.99
Imputation 6	0.82	0.59	0.55	0.79	0.97	0.99
Imputation 7	0.82	0.62	0.54	0.81	0.97	0.99
Imputation 8	0.82	0.59	0.56	0.79	0.97	0.99
Imputation 9	0.82	0.61	0.55	0.80	0.97	NA
Imputation 10	0.82	0.59	0.57	0.80	0.97	0.99
<i>Average</i>	<i>0.82</i>	<i>0.60</i>	<i>0.59</i>	<i>0.80</i>	<i>0.97</i>	<i>0.99</i>
<i>Balanced accuracy</i>	<i>0.50</i>	<i>0.56</i>	<i>0.57</i>	<i>0.55</i>	<i>0.50</i>	<i>0.50</i>



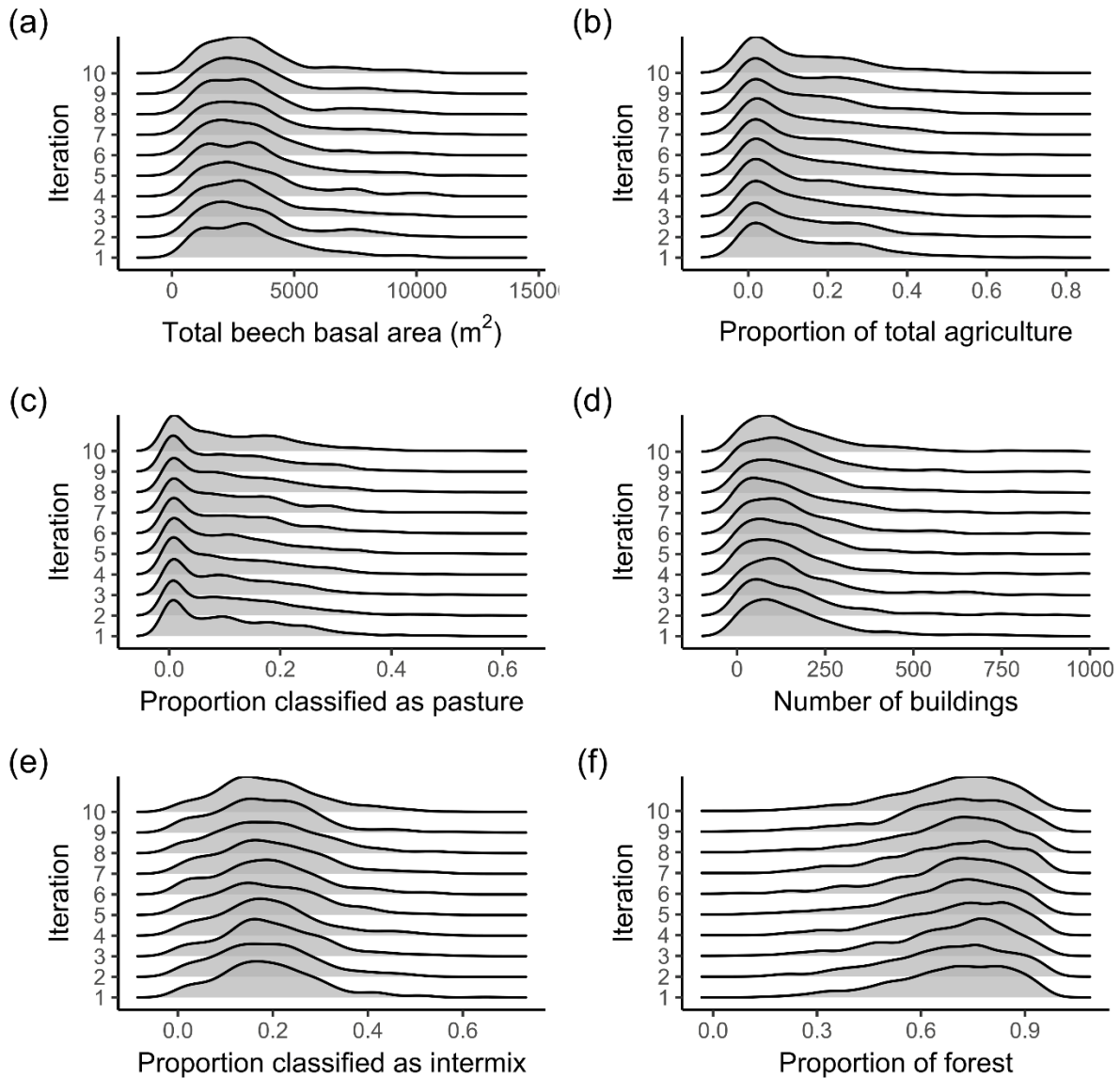
**Table A5.** Coefficients from logistic regression models estimating probability of exposure to each of the three most commonly detected anticoagulant rodenticide compounds (on logit scale).

Bolded coefficients were interpreted as statistically significant.

Coefficient	Mean	Standard Error	Z-score	2.5%	97.5%
<i>Brodifacoum</i>					
Intercept	0.656	0.212	3.098	0.241	1.071
Sex (M)	0.430	0.270	1.592	-0.099	0.960
<b>Age</b>	<b>1.077</b>	<b>0.184</b>	<b>5.842</b>	<b>0.716</b>	<b>1.438</b>
<b>Age<sup>2</sup></b>	<b>-0.352</b>	<b>0.094</b>	<b>-3.764</b>	<b>-0.536</b>	<b>-0.169</b>
<b>Intermix (15 km<sup>2</sup>, 100 m)</b>	<b>0.340</b>	<b>0.147</b>	<b>2.315</b>	<b>0.052</b>	<b>0.627</b>
Pasture (15 km <sup>2</sup> )	-0.225	0.156	-1.430	-0.530	0.081
Beech basal area (15 km <sup>2</sup> )	0.099	0.177	0.578	-0.248	0.446
Lagged beechnuts	0.002	0.127	0.016	-0.247	0.251
Basal area × beechnuts	-0.062	0.131	-0.482	-0.318	0.194
<i>Bromadiolone</i>					
Intercept	-0.733	0.199	-3.693	-1.122	-0.344
Sex (M)	0.317	0.272	1.165	-0.216	0.850
<b>Age</b>	<b>0.584</b>	<b>0.191</b>	<b>3.067</b>	<b>0.211</b>	<b>0.958</b>
<b>Age<sup>2</sup></b>	<b>-0.287</b>	<b>0.124</b>	<b>-2.307</b>	<b>-0.530</b>	<b>-0.043</b>
<b>Intermix (15 km<sup>2</sup>, 100 m)</b>	<b>0.336</b>	<b>0.138</b>	<b>2.421</b>	<b>0.066</b>	<b>0.605</b>
Pasture (15 km <sup>2</sup> )	0.128	0.154	0.847	-0.174	0.430
Beech basal area (15 km <sup>2</sup> )	0.167	0.162	1.021	-0.151	0.485
<b>Lagged beechnuts</b>	<b>0.325</b>	<b>0.132</b>	<b>2.472</b>	<b>0.067</b>	<b>0.583</b>
Basal area × beechnuts	-0.003	0.135	-0.038	-0.268	0.262
<i>Diphacinone</i>					
Intercept	1.292	0.211	6.136	0.879	1.705
<b>Sex (M)</b>	<b>0.718</b>	<b>0.308</b>	<b>2.332</b>	<b>0.115</b>	<b>1.322</b>
<b>Age</b>	<b>0.962</b>	<b>0.198</b>	<b>4.860</b>	<b>0.574</b>	<b>1.350</b>
<b>Age<sup>2</sup></b>	<b>-0.347</b>	<b>0.097</b>	<b>-3.596</b>	<b>-0.536</b>	<b>-0.158</b>
Intermix (15 km <sup>2</sup> , 100 m)	0.216	0.156	1.383	-0.090	0.522
Pasture (15 km <sup>2</sup> )	-0.058	0.158	-0.363	-0.368	0.252
Beech basal area (15 km <sup>2</sup> )	0.052	0.178	0.284	-0.296	0.401
Lagged beechnuts	0.095	0.135	0.705	-0.169	0.359
Basal area × beechnuts	-0.056	0.141	-0.404	-0.333	0.221
<i>Dicoumarol</i>					
Intercept	-3.081	0.339	-9.085	-3.746	-2.416
<b>Sex (M)</b>	<b>1.044</b>	<b>0.464</b>	<b>2.253</b>	<b>0.135</b>	<b>1.952</b>
Age	-0.071	0.254	-0.280	-0.568	0.426
Pasture (15 km <sup>2</sup> )	0.037	0.229	0.188	-0.411	0.486

Variance of random effect brodifacoum (WMU): 0.20  
Variance of random effect bromadiolone (WMU): 0.09  
Variance of random effect diphacinone (WMU): 0.11  
Variance of random effect dicoumarol (region): 0.05

### Appendix 3-3: Consistency of covariate values among imputed datasets



**Figure A1.** Variability of covariate value densities between point iteration sets. X-axis values represent covariates within a 15, 30 or 60 km<sup>2</sup> buffer at each random point location: (a) total beech basal area, (b) proportion of buffer classified as pasture/hay or cultivated crops, (c) proportion of buffer classified only as pasture/hay, (d) number of building centroids within the buffer, (e) proportion of buffer classified as WUI intermix, and (f) proportion of buffer classified as forest. X-axis was truncated for number of buildings to remove outliers >1000.

## **CHAPTER 4: DRIVERS OF ANNUAL SURVIVAL IN FISHERS ACROSS LANDSCAPE GRADIENTS**

### **ABSTRACT**

Estimates of demographic rates, and knowledge of their drivers, are important for conserving wildlife populations. Survival rates of carnivores, including mustelids, are generally linked to prey availability, inter- and intraspecific competition, and human activity—factors likely to vary considerably across heterogeneous landscapes. Across northern New York State, populations of fisher (*Pekania pennanti*) range from high to low density across a gradient of forest productivity and human land use. Across this gradient we investigated sex and age-specific survival rates, and landscape drivers, using data from 146 collared individuals between January 2019 and December 2022. As expected, survival rates pooled across the gradient were higher for female versus male fisher, and for adults versus juveniles. Annual Kaplan-Meier survival rates, pooled across age and sex, were 1.4x times higher in the low-density Adirondack population. Cumulative incidence functions indicated 5.2x higher harvest mortality in the high-density population and 2.0x higher non-harvest mortality in the low-density population. We investigated spatial determinants of overall and cause-specific (i.e., harvest versus non-harvest) mortality risk via a Bayesian proportional hazards model formulated as a counting process. Apparent habitat quality, based on probability of selection, explained the most variation in annual survival rates; however, considerable uncertainty in model selection indicated an overall gradient of annual mortality risk not explained by one specific landscape variable. Harvest mortality risk increased in areas of higher habitat quality. Additionally, harvest mortality, and to a lesser extent, non-harvest mortality increased in mast failure years and decreased in areas with greater human development.

We suggest variation in prey availability or abundance, as quantified by variation in landscape gradients, is driving fisher survival across northern New York.

## **INTRODUCTION**

Understanding what drives changes in population growth rate is fundamental to ecology and management of wildlife (Linnell and Strand 2000), in part because there is variability among species and groups of species regarding which vital rates drive variation in population growth rate (Sæther and Bakke 2000, Bellier et al. 2018). Management and conservation actions generally aim to safeguard the demographic rate that has the strongest contribution to population growth rate (Wilson et al. 2016, Koons et al. 2017). Often, species with slow life histories, characterized by late sexual maturity and lower reproduction rates, are maintained by high survival rates that display relatively little year-to-year variation (Pfister 1998, Healy et al. 2019). Yet, demographic rates, including survival, can vary across a species' range due to phenotypic plasticity (Coulson et al. 2005) or individuals experiencing gradients in ecological variation that result in different population trends (Pulliam 1988). A better understanding of spatial variability in demographic rates will be increasingly important to the effective management of animal populations in a changing world, especially for carnivores—generally slow-tempo species—that depend on prey affected by changing landscapes (Wolf and Ripple 2016).

Carnivore populations are closely linked to prey densities because prey abundance and availability are important drivers of both reproduction and survival rates (O'Donoghue et al. 1997, Fuller and Sievert 2001, Ford et al. 2010, Svoboda et al. 2019). Such bottom-up control of carnivore populations is also likely linked to abiotic conditions (Pozzanghera et al. 2016), demonstrating the complexity of factors that may be driving carnivore survival rates. Low prey

availability can also indirectly lead to higher mortality, for example by increasing susceptibility to trapping or vehicle collision due to individuals being required to increase their foraging area (Brand and Keith 1979, Jensen et al. 2012). Spatial and temporal heterogeneity in the abundance and availability of prey may be linked to inter- and intraspecific competition (Herfindal et al. 2005). For example, greater overlap in diet often leads to greater intraguild killing via higher encounter rates between predators searching for the same prey (Polis 1988). Thus, carnivore populations are often controlled by bottom-up conditions (prey) as well as top-down forces such as predation and harvest.

Many carnivores, and mustelids in particular, occur at low densities and are often susceptible to overharvest (Aubry and Lewis 2003). Harvest pressure resulting in even slightly additive mortality may cause declines in carnivore abundance (Powell 1979). Spatial dynamics of harvested populations may mitigate negative effects, in that areas that have limited access by trappers may act as de facto refugia and sources for new animals in more heavily harvested populations (Strickland 1994, McCullough 1996), and harvest pressure often varies with accessibility by hunters and trappers (Hiller et al. 2011, Wiebe et al. 2013). Yet, in many populations, harvest can be additive such that harvest mortalities increase the annual mortality rate instead of compensating for the individuals that would have likely died anyway of natural causes (Anderson and Burnham 1976, Burnham and Anderson 1984). Collectively, these factors necessitate close monitoring of harvested carnivore populations given potential for the cumulative effects of harvest and natural mortality on population growth rate.

In fishers (*Pekania pennanti*), adult survival—especially of individuals  $\geq 3$  years—is predicted to have the greatest impact on population persistence (Ferguson and Larivière 2002, Buskirk et al. 2012). Juveniles are generally a vulnerable group (Soukkala 1983, Krohn et al.

1994, Strickland 1994). Given increased distances traveled during dispersal (Fuller and Sievert 2001) and naivety to the risk of hunters and trappers (e.g., Clausen et al., 2017), juveniles often represent a high proportion of annual harvests (Strickland 1994)—yet survival of individuals up to one year old is also important in maintaining population growth rates in fisher (Buskirk et al. 2012). Across heterogeneous landscapes, there are numerous factors that can influence fisher survival and subsequent population trends. Major sources of non-harvest mortality include intraguild killings by larger sympatric carnivores (Wengert et al. 2014, Gabriel et al. 2015), with smaller-bodied females being more vulnerable to predation than males (Sweitzer et al. 2016*b*). Starvation is another major mortality source (Sweitzer et al. 2016*a*), stemming from resource limitation and intra- or interspecific competition. Non-harvest but nonetheless human-caused mortality sources include vehicle strikes and growing concerns regarding rodenticide poisoning (Thompson et al. 2014, Sweitzer et al. 2016*b*). Although diseases, such as rabies or canine distemper, also result in fisher mortalities they are not a primary concern for the species (Powell et al. 2003, Larkin et al. 2010). Thus, there are a number of potentially interacting factors that may influence fisher survival across a landscape.

Herein, we investigated fisher mortality across northern New York State, a heterogeneous region sharing many ecological characteristics (e.g., a predominantly northern hardwood forest) that also differ in forest management history, abiotic conditions, human land use intensity, and apparent fisher population density (New York State Department of Environmental Conservation 2015). Catch-per-unit-effort (CPUE) data have presumably indicated low density fisher populations in the inner Adirondack Park region compared with areas to the immediate west and south (New York State Department of Environmental Conservation 2015, Linden et al. 2017). We hypothesized that the observed patterns in CPUE were due to differences in demographic

rates, especially survival. Therefore, our objectives were to 1) determine age-, sex-, and focal area-specific survival rates, 2) identify spatial characteristics contributing to differences in mortality risk, and 3) examine drivers of cause-specific mortality (i.e., harvest vs. non-harvest). Because previous work has indicated lower probability of selection for habitats in the inner Adirondack Park (Jensen and Humphries 2019), we explored several metrics that we predicted would be related to prey availability. We predicted that older forests would negatively impact survival rates due to low prey abundances (Potvin et al. 2005). We expected that proximity to human development, via increased road density or housing density, would be related to increased risk of mortality via vehicle strikes, harvest mortality (i.e., trapper access), or rodenticide poisoning. Additionally, interannual trapping vulnerability in mustelids has been linked to hardwood mast cycles due to variation in prey populations (Jensen et al. 2012, Greenhorn et al. 2021). Therefore, we predicted greater mortality in mast failure years. While fishers often have difficulty hunting in deep snow (Leonard 1980, Raine 1983), winter severity has been shown to be a strong predictor of deer survival (DelGiudice et al. 2002), and fishers depend on deer carrion as a major source of food in the winter when other prey is scarce (Allen et al. 2021). The presence of coyotes (*Canis latrans*) may facilitate fisher access to deer carcasses, though we also predicted that the high relative abundances of coyotes may present an increase mortality risk to fishers.

## **STUDY AREA**

We conducted our work across northern New York State (Fig. 1), with two field teams operating in separate focal areas—the Tug Hill Plateau (74.25583° W, 43.88097° N; 2,287 km<sup>2</sup>) and the inner Adirondack Park (75.73783° W, 43.63153° N; 9,506 km<sup>2</sup>). While not physically connected, the Tug Hill Plateau and Adirondack focal areas represent the same general ecoregion



(Hansen et al. 2015), representing a transitional zone between temperate and boreal forests (Evans and Brown 2017) and consists of northern hardwoods (e.g., sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], and American beech [*Fagus grandifolia*]), spruce-fir (e.g., red spruce [*Picea rubens*] and white pine [*Pinus strobus*]), and mixed hardwood/coniferous forest types (Bryce et al. 2010). As such, we considered our two focal areas within the context of potential gradients of conditions across northern New York, which often show east-to-west variation in habitat characteristics such as elevation, annual snow accumulation, and average forest stand age, amongst others (Fig. 2). The Adirondack Park is a ~24,000 km<sup>2</sup> mixture of private and public land, nearly half of which is protected from development or forest management of any kind (McMartin 1999, Kretser et al. 2008) due to the ‘Forever Wild’ clause in the New York State Constitution (Keal and Wilkie 2003). The Tug Hill Plateau has greater amounts of private land and anthropogenic development, but still contains over 550 km<sup>2</sup> of state forest and other public lands, though the surrounding lowlands primarily support agriculture. The elevation varies from 200–1,600 m above sea level, though terrain was mountainous in the east and more even in the west. The area supports a variety of fisher prey species in various densities, including North American porcupines (*Erethizon dorsatum*), snowshoe hares (*Lepus americanus*), American red squirrels (*Tamiasciurus hudsonicus*) and white-tailed deer (*Odocoileus virginianus*). Sympatric carnivores include coyotes, American marten (*Martes americana*), and bobcats (*Lynx rufus*). Fisher harvest was permitted throughout the entirety of both focal areas, though season dates and lengths differed slightly.

Climate conditions were typical of northeastern United States. Annual minimum temperatures ranged from –2.6–4.2 and maximum temperatures ranged from 7.6–14.6 °C (PRISM Climate Group Oregon State University 2022). During the winter, the Tug Hill Plateau

and western Adirondack mountains were subject to frequent and intense lake-effect snowstorms due to its location directly east of Lake Ontario (Veals and Steenburgh 2015). The annual snow accumulation (15-year average) for our focal areas ranged from 152–673 cm (National Operational Hydrologic Remote Sensing Center 2023).

Northern New York offers substantial opportunities for recreational use, including hunting and trapping. The trapping season throughout much of northern and southeastern New York, including the Tug Hill Plateau, is 46 days long (25 October–10 December), while trapping is allowed for only 30 days in the Adirondack region (1–30 November). There are no bag limits for fishers, but restrictions on trap types and lure use are implemented during seasons for other terrestrial furbearers minimize unintended trapping of fishers outside of the 46- or 30-day trapping seasons (New York State Department of Environmental Conservation 2015).

## **METHODS**

### ***Fisher captures and monitoring***

Our live-trapping season ran from 25 October to approximately 7 March every winter, between January 2019 and March 2022. Trapping was conducted by New York State Department of Environmental Conservation (NYS DEC) staff, but we also utilized the knowledge and experience of long-time recreational trappers, contracting with them to use live traps to catch animals for our study instead of harvesting fishers for pelts. Contract trappers were selected by DEC biologists and required to attend an orientation session and follow trapping guidelines. Traps were set near roads or snowmobile trails, generally in pairs. Fishers were captured using Tomahawk box traps model 108 (Tomahawk Live Trap, Hazelhurst, WI, USA) enclosed by black coroplast and lined with sheep's wool and baited with beaver (*Castor canadensis*) or moose (*Alces alces*) meat and commercial scent lure. Fishers were immobilized with ketamine

hydrochloride and xylazine hydrochloride and reversed with yohimbine or atipamezole hydrochloride (see Cunningham et al. 2022 for additional details). When possible, we processed fishers at the capture site, but during inclement weather or multiple capture events we transported fishers to a central location for processing but released them from the original trap site upon recovery from anesthesia. We estimated fisher age during processing based on tooth wear and in females, nipple size (Paragi 1990, Frost et al. 1999, Green et al. 2017), but also extracted a tooth (PM1) for later age determination by cementum annuli analysis (Fancy 1980, Arthur et al. 1992) at Matson's Laboratory (Manhattan, MT, USA). Blood samples from a subset of trapped fisher were drawn from the jugular vein for prothrombin time testing via a dilute canine assay at the Comparative Coagulation Section of the Animal Health Diagnostic Center at Cornell University. We obtained measurements of anesthetized fishers, including weight and body length, which we used to calculate a body condition index as described later.

Adult female fishers were fitted with Lotek LiteTrack Global Positioning System (GPS) Collars (40 g; Lotek Wireless, Newmarket, ON, Canada) for fine-scale monitoring during an associated study on productivity. Juveniles (both sexes) and adult male fishers were fitted with ATS M1940 VHF collars (42 g; Advanced Telemetry Systems, Isanti, MN, USA). Beginning October 2020, we affixed GPS loggers (GPS CatLog2, 35 g; Perthold Engineering, Dallas, TX, USA) to a subset of VHF collars for male fishers with epoxy and rubber shrink tubing. Collared fishers received a numbered metal tag in each ear (National Band and Tag Company, Newport, KY, USA). All collars included text with a phone number and noting that a reward would be offered for their return, so we therefore assumed high return rates for any fishers harvested in subsequent years (Royle and Garrettson 2005). Additionally, the DEC requires trappers to submit each pelt for sealing prior to sale or transport, so we presumed all legally harvested fishers that

retained their ear tags would be identified, in addition to those that were harvested with their collar. We added reflective tape to collars in unique patterns for incidental photo capture and identification. Both collar types were equipped with mortality signals that activated after eight hours of no movement.

We searched for all individuals at least monthly via VHF telemetry, either from a vehicle or a fixed-wing aircraft (Cessna 172, Textron Aviation, Wichita, KS, USA). We also included opportunistic camera trap photos of collared individuals as relocations. Aerial locations were recorded at the point a telemetry signal was first detected, and we assumed the collared animal was within 3.2–4.0 km based on observed distances from test collars. If a mortality signal was detected, efforts were made to physically find the animal as soon as possible, generally within three days. Intact carcasses were sent to the DEC Pathology Lab in Delmar, NY or to the Wildlife Health Lab at Cornell University in Ithaca, NY for necropsy, pathology, and toxicology screening. Overall, we were conservative in our attribution of mortality to specific sources, marking most as unknown.

We removed individuals from survival analyses if they died during capture ( $N = 2$ ) or within 7 days of capture to eliminate bias due to capture effects (Smith et al. 2022). We also excluded fishers that were captured but released with ear tags only ( $N = 7$ ), without a collar ( $N = 2$ ), or those that were collared but never relocated after release ( $N = 16$ ). We used a recurrent time scale for annual survival estimates (Fieberg and DelGiudice 2009) beginning on 1 April and ending 31 March, as fishers are born in March and early April (Green et al. 2018). We considered fishers to be at risk the day after capture, and mortalities were recorded on the date (if known), or the midpoint between the date the carcass was found and the last known alive date (DeCesare et al. 2016). For 3 individuals we could not determine if they were dead or dropped

their collar, so we censored them after the midpoint between the date the collar was found and the last known alive location. When radio signals were lost (i.e., fishers became lost-to-follow-up), we right-censored individuals after the last known location.

### ***Individual condition and spatial covariates***

We tested three metrics related to individual condition for linkages to survival. We accounted for the effects of age by including a binary variable for adults and immatures. Blood samples (N = 70) were tested for prothrombin time to assess clotting time. Blood clotting has been shown to be indicative of rodenticide exposure in raptors (Hindmarch et al. 2019), and there was no otherwise available assay for direct rodenticide testing on live animals. We calculated a body condition score (BCS) using mass divided by body length (g/cm; Jakob et al. 1996, Rosas et al. 2009) for fishers with measurements (N = 120). We accounted for differences in sex via and interaction term in the BCS model because scores showed a strongly bimodal distribution. To model the association of survival with measurements, we assigned measurements to encounters within one year of capture. Individual covariates were modeled separately from landscape covariates.

We developed a set of six *a priori* hypotheses to explain variation in fisher survival rates across northern New York, using spatial variables related to habitat quality, prey availability, predator competition, and human encroachment into forests (Table 1). For each spatial covariate, we generated 5-, 20-, 40-, and 60-km<sup>2</sup> circular buffers around live and mortality locations to both represent the general spatial characteristics of the landscapes each fisher inhabited and to account for uncertainty in fisher locations determined via telemetry. Buffers were generated via the *sf* package (Pebesma 2018), and variable extraction completed with the *terra* (Hijmans 2021) and *exactextractr* (Bastou 2022) packages in R v. 4.3.1 (R Core Team 2023). We summarized

average forest stand age from a layer developed from Forest Inventory and Analysis data (Wilson et al. 2018). We also assessed probability of selection as a measure of habitat quality, based on a resource selection probability function developed by Jensen and Humphries (2019). We predicted that coyote relative abundance could represent competition between species, potential predation by the coyotes, or food provisioning by coyotes via deer carcasses. The coyote relative abundance layer was based on camera trap detections across northern New York and a Royle-Nichols model (Royle and Nichols 2003; J. Twining, unpublished model).

To characterize the human impact of fisher habitat that may be related to survival, we used the wildland-urban interface (WUI). WUI represents the juxtaposition of man-made structures and wildland vegetation (e.g., NLCD forest, shrubland, grassland/herbaceous, and wetland classes; Radeloff et al. 2005, Stewart et al. 2007), and is generally classified as intermix WUI, interface WUI, or non-WUI (Bar-Massada et al. 2014). We used a  $30 \times 30$  m layer developed by Carlson et al. (2022) that had a search radius of 250 m. The focal pixel was classified as intermix WUI when the search radius contained  $>50\%$  wildland vegetation and building densities  $>6.17$  units/km<sup>2</sup> (i.e., 2 buildings within the radius), classified as interface WUI when building densities were  $>6.17$  units/km<sup>2</sup> and within 2.4 km of a  $\geq 5$  km<sup>2</sup> patch containing  $\geq 75\%$  wildland vegetation, and non-WUI otherwise (Bar-Massada et al. 2013, Carlson et al. 2022). We considered WUI to be a binary variable, either WUI (intermix and interface) or non-WUI and calculated the percent of each buffer classified as WUI for our analyses.

In addition to spatial layers, we included a binary variable depicting mast year or mast failure in some of our models. The Huntington Wildlife Forest (44°00'N, 74°13'W) at SUNY College of Environmental Science and Forestry maintains an annual index of beech mast

production collected between July and November. During our study, 2019 and 2021 were mast years, while 2020 and 2022 were mast failure years. We also calculated a winter severity index (WSI) to represent potential food availability from deer carcasses during the winter. The index, based on DelGiudice et al. (2002), was a cumulative score that increased by one point whenever the minimum daily temperature was below  $-17.7^{\circ}\text{C}$  or snow depth exceeded 38 cm. We used daily Global Historical Climatology Network (Menne et al. 2012*b, a*) station data for snow depth (cm). We filtered stations that had fewer than 200 days of the 212-day winter season and used the forecast package (Hyndman and Khandakar 2008, Hyndman et al. 2023) to interpolate any remaining missing snow depth values. Because nearly 70% of expected minimum temperature values were missing from the weather station data, we used minimum temperature NCEP Reanalysis II data (Kanamitsu et al. 2002), extracted at weather station points. The median distance of fisher locations to the closest weather station was 9.3 km. We centered and scaled all continuous variables prior to model fitting.

We used the Bayesian latent indicator scale selection (BLISS) process to determine scale (i.e., 5, 20, 40, or 60  $\text{km}^2$ ) for each spatial covariate based on posterior probabilities (Stuber et al. 2017). This process uses a reversible-jump Markov Chain Monte Carlo (RJMCMC) algorithm to examine models with different parameter space (i.e., swapping out model components), and therefore does not face issues of collinearity between scales. We implemented the BLISS procedure in JAGS v. 4.3.1 (Plummer 2003) via the *rjags* package v. 4-14 (Plummer 2023) in R (R Core Team 2023), sampling from one chain for 20,000 iterations, burning the first 5,000 and without thinning. We set prior weights to be equal across all spatial scales.

### *Survival analysis*

We used a Bayesian proportional hazards model (Cox 1972, Ibrahim et al. 2001, Jones et al. 2020) to quantify the mortality risk of fishers across northern New York. The Bayesian proportional hazards model was formulated as a counting process to allow for time-varying spatial covariates to explain mortality risk (Andersen and Gill 1982). In this framework, we modeled observed mortalities ( $dN_{ij}$ ) for each individual  $i$  at failure time  $j$  as a Poisson random variable with a mean intensity  $d\Lambda_{ij}$  (Jones et al. 2020). The baseline hazard  $d\Lambda_{ij}$  followed a gamma distribution with parameters  $\mu_j$ , the mean prior estimate, and  $c$ , a dispersion parameter related to the strength of the prior knowledge (see Jones et al. [2020] for additional details on model specification). We used normal priors with mean of 0 and standard deviation of 100 for log hazard coefficients ( $\beta$ ).

The Bayesian proportional hazards model allowed us to estimate annual survival probabilities equivalent to the Kaplan-Meier estimator adjusted for staggered entry (Pollock et al. 1989). For annual survival, we retained individuals in the risk set during periods with missed detections, as removing these animals could result in negative bias of the survival estimates, while imputing the status of the individual from a later detection should not bias estimates (DeCesare et al. 2016). We estimated annual survivorship for all fishers pooled across both focal areas, as well as age, sex, and focal area-specific survival probabilities. We estimated annual survival probabilities for immature (<2 years) and adult ( $\geq 2$  years) fishers. All collared fishers were  $\geq 6$  months old. Next, we used the results of the BLISS approach to examine the relationship between mortality risk and our hypotheses. In addition to the six hypotheses related to annual survival, we also investigated season-specific mortality risk related to fisher-coyote relationships, dividing the year into summer (April–October) and winter (November–March).



Though we implemented our models in a Bayesian framework, we used the *survival* package (Therneau and Grambsch 2000, Therneau 2021) to check that proportional hazards assumptions were met. We considered group-specific survival probabilities to be significantly different if there was no overlap of 95% Bayesian credible intervals, and for covariates to be impactful if 95% of the posterior samples were the same sign as the mean. We report hazard ratios (HR) to indicate an increased ( $>1.0$ ), decreased ( $<1.0$ ), or no difference ( $=1$ ) in probability of mortality.

We estimated cumulative incidence functions (CIF) within the Bayesian proportional hazards framework to describe mortality risk for harvest and non-harvest sources (Heisey and Patterson 2006) in each focal area. We followed procedures described in Jones et al. (2020) to code observations for each of the two mortality sources (i.e., harvest and non-harvest). We also investigated the effects of habitat quality, mast failure, and WUI on harvest and non-harvest mortality sources within a competing risks framework. We implemented survival models in JAGS v. 4.3.1 (Plummer 2003) via the *jagsUI* package (Kellner 2021) in R (R Core Team 2023). We used the ``autojags()`` function to run models until convergence ( $\hat{R} < 1.1$ ), updating three chains with 1,000 iterations at each increment with a burn-in of 1,000. We compared models via the widely applicable information criterion (WAIC; Watanabe 2013) using the *loo* package v. 2.6.0 (Vehtari et al. 2017, 2023).

Finally, we assessed the estimated survival rates in the context of population dynamics by calculating the number of juveniles necessary to maintain a stable or increasing population, given estimated survival of mature female fishers (Koen et al. 2007). We used a variant of Lotka's equation described by Henny et al. (1970) and simplified by Paragi et al. (1994) to

$$1 = m \times S_0 \times S + S, \quad (1)$$

where  $m$  is the number of female fisher kits produced by adult females and that are recruited into the population by the autumn trapping season,  $S_0$  is the annual survival of juvenile female fishers (<1 year old), and  $S$  is the survival of female fishers  $\geq 1$  year old. Setting the right-hand side of the equation equal to 1 assumed a stable population (i.e., finite rate of increase  $[\lambda] = 1$ ). Because our live-trapping season coincided with the start of the fisher harvest season and we only trapped fishers  $\geq 6$  months old, we could not obtain empirical estimates of  $S_0$ . Therefore, used a range of values for  $S_0$  (0.14–0.50) based on the confidence interval of estimated survival rates from Paragi et al. (1994).

## RESULTS

We collared 177 individual fishers across both focal areas (Table 2), including 11 that were recaptured  $\geq 1$  year after original capture event, but excluded from our analyses 4 individual that died within 7 days of collaring and 16 that were never relocated after collaring (including four during the Covid-19 pandemic shutdown in March-June 2020). Most fishers were relocated after telemetry flights resumed in July 2020, despite cessation of monitoring during the spring.

However, 8 individuals may have been lost-to-follow-up as a result of the Covid-19 pandemic lockdowns. Ultimately, our final risk set included 67 fishers in the Adirondack focal area and 79 in the Tug Hill Plateau focal area, yielding a total sample size of 146 (Table 1). We obtained cementum annuli-based ages from 121 (83%) fishers in our risk set, and used field-based age estimates for the remaining 25 fishers. We permanently right-censored 67 fishers that were lost-to-follow-up prior to the end of the study due to collar loss, collar failure, or dispersal from the focal areas. At the end of the study, we right-censored the 22 fishers that remained in the study. We observed 57 deaths (22 Adirondack, 35 Tug Hill) over our study period (Table 1).

Our estimates of annual survival included a total of 127.2 fisher risk-years, and individuals were at risk for a median of 0.75 years (SD = 0.63). The pooled dataset yielded an average annual survival rate ( $\hat{S}$ ) of 0.61 (95% Bayesian credible interval [BCI] 0.53, 0.69; N = 146). Female fishers tended towards higher average survival rates ( $\hat{S} = 0.66$ , 95% BCI 0.54, 0.76, N = 68) than males ( $\hat{S} = 0.57$ , 95% BCI 0.46, 0.68; N = 78), but with considerable overlap of 95% confidence intervals between the two sexes. Estimates of annual survival were highest for adults ( $\hat{S} = 0.67$ , 95% BCI 0.55, 0.77; N = 74) and lower for fishers  $\leq 2$  years of age ( $\hat{S} = 0.49$ , 95% BCI 0.36, 0.63; N = 99). On average, fishers in the Adirondack focal area, which was presumed to have a lower density, had higher survival rates ( $\hat{S} = 0.71$ , 95% BCI 0.60, 0.80 N = 67) than the Tug Hill Plateau focal area ( $\hat{S} = 0.52$ , 95% BCI 0.40, 0.63; N = 79; Figure 2), with marginal overlap of credible intervals (Fig. 3). We did not observe strong impacts of individual-level health indicators on risk of mortality. Prothrombin time (Hazard ratio [HR] = 0.31, 95% BCI 0.06, 1.68; N = 70) at the time of capture was not a significant predictor of mortality risk. After accounting for the effects of sex, body condition score was also not a predictor of mortality (HR = 0.77, 95% BCI 0.15, 2.53; N = 120). However, the number of deaths was low for both blood tests (7) and body condition (10), so we suspect that our power to detect effects was lower than models including spatial variables.

The BLISS procedure identified landscape variables at the 20, 40 and 60 km<sup>2</sup> scales (Table 1). The top model determined by WAIC was the model for hypothesis 1, which included habitat quality (based on a resource selection probability function by Jensen and Humphries [2019]) as a spatial predictor and age (Table 3). However, the models including coyote relative abundance, stand age, and the null model (including age effects only) were all within 2  $\Delta$ WAIC, indicating that not one clearly explained spatial variation in fisher survival. The top model

indicated that risk of mortality increased in areas of high habitat quality (i.e., high probability of selection), though confidence in strength of the effect is moderate (HR = 1.47, 95% BCI 0.58, 3.05). The next best model showed a decreased risk of mortality in older stands (HR = 0.80, 95% BCI 0.45, 1.36), though our confidence in the strength of the effect is low because the 95% credible interval overlapped 1. Finally, risk of mortality increased in areas with greater coyote relative abundance, but again with moderate confidence (HR = 1.47, 95% BCI 0.82, 2.40). When we considered seasonal survival related to coyote relative abundance, summertime risk of mortality increased with increasing coyote abundance, though variation was high (HR = 1.46, 95% BCI 0.56, 3.18). In the winter, we observed, with high confidence, an interaction between coyote relative abundance and WSI (HR = 0.02, 95% BCI 0.001, 0.10).

For the 57 mortalities retained in the risk set, known cause of death included harvest, disease (rabies), rodenticide poisoning, vehicle strike, and predation (Table 4). However, 40% of mortalities could not be attributed with confidence to a specific cause. Harvest was the cause of death for 49% of collared fishers, though only 4 of the 28 harvested fishers came from the Adirondack focal area. Based on our cause-specific mortality analysis, data from the two study areas pooled indicated that there was no difference in mortality from harvest (CIF = 0.27, 95% BCI 0.18, 0.39; N = 28) or non-harvest sources (CIF = 0.22, 95% BCI 0.15, 0.32; N = 29). Yet, fishers captured within the Adirondack Park had rates of non-harvest mortality (CIF = 0.30, 95% BCI 0.18, 0.47) that were nearly double that of fishers in the Tug Hill Plateau focal area (CIF = 0.15, 95% BCI 0.07, 0.27), while Tug Hill fishers experienced rates of harvest mortality (CIF = 0.42, 95% BCI 0.27, 0.63) that were over 5 times higher than Central Adirondack fishers (CIF = 0.08, 95% BCI 0.03, 0.20). An increase in habitat quality was associated with a strong increase in mortality risk due to harvest (HR = 15.1, 95% BCI 3.23, 52.1), but we did not

observe a similar impact on non-harvest mortality (HR = 1.09, 95% BCI 0.49, 2.27). However, the risk of mortality decreased for harvest (HR = 0.31, 95% BCI 0.09, 0.75) and non-harvest mortality (HR = 0.37, 95% BCI 0.10, 0.88), with high confidence, in areas of WUI. Finally, risk of mortality increased in mast failure years compared to years with mast crops, with a stronger effect seen for risk of harvest mortality (HR = 3.46, 95% BCI 1.27, 8.34) compared to non-harvest mortality (HR = 1.72, 95% BCI 0.74, 3.52).

Survival of female fishers  $\geq 1$  year old was lower in the Tug Hill (0.62, 95% BCI 0.46, 0.77) than in the Adirondack (0.76, 95% BCI 0.57, 0.89) focal area. Based on the posterior medians and 95% credible interval for each focal area, litter size for each female ( $2m$ , assuming a 1:1 sex ratio) necessary to maintain a stable population ranged from 2.51 (95% BCI 1.12, 5.33;  $S_0 = 0.50$ ) to 8.98 (95% BCI 4.00, 19.02;  $S_0 = 0.14$ ) kits for the Tug Hill focal area and 1.37 (95% BCI 0.42, 2.92;  $S_0 = 0.50$ ) to 4.89 (95% BCI 1.50, 10.43;  $S_0 = 0.14$ ) kits for the Adirondack focal area (Figure 4). Assuming an average juvenile survival rate ( $S_0$ ) of 0.27 estimated by Paragi et al. (1994), a stable population growth rate would require litter sizes of 4.65 (95% BCI 2.07, 9.86) in the Tug Hill and 2.54 (95% BCI 0.78, 5.41) in the Adirondack focal area.

## **DISCUSSION**

Across northern New York State, we estimated overall survival rates for fisher that fall on the lower end of, but not outside of, published estimates elsewhere within northeastern North America (Lewis et al. 2022)—a somewhat surprising result given fairly rapid rates of fisher population expansion in recent decades documented across NY State (NYSDEC unpublished data). Overall, we observed an increase of 0.19 (95% BCI 0.03, 0.33) in the probability of

survival between Tug Hill and Adirondack focal areas (with marginal overlap in credible intervals)—areas we expected to differ considerably in terms of overall system productivity. However, while overall mean survival rates across our study area were highest in the Adirondack focal area, fishers in the more human-dominated Tug Hill Plateau focal area were at greater risk of harvest whereas fishers in the more remote Adirondack region remained more susceptible to non-harvest sources of mortality (including natural mortality and other anthropogenic mortality). These results also were surprising, as we anticipated harvest as a percentage of mortality to be higher in the lower density Adirondack population. However, even the lesser amount of harvest on the lower density population may contribute inordinately to population growth due to other mitigating factors, such as disproportionately high harvests of adults compared to juveniles.

Generally, immature individuals are expected to represent a greater proportion of harvest than adults, which is thought to be largely compensatory to natural mortality experienced by immature fishers (Krohn et al. 1994). The median age at harvest for fishers, aged in this study via cementum annuli analysis, was 1.6 years old (N = 24). We obtained cementum annuli-based age estimates for three of the 4 fishers harvested from the Adirondack focal area, and all were 1.6 years old or older, with the remaining fisher estimated at capture to be an adult. Similarly, the live-captured individuals were skewed towards older individuals in the Adirondack Park, while we captured many more fishers that were <1 year old in the Tug Hill Plateau (Table 5). Lower overall catch per unit effort combined with the lower ratio of juveniles:adults in our live capture efforts indicate the potential for harvest of fisher in the Adirondack focal area to be more additive than compensatory (Lebreton 2005). While fisher populations are generally thought to be robust to an annual take of 15–25% (Douglas and Strickland 1987), small and low-density fisher populations can be at risk of extinction when even 10% of the population is removed

(Fogarty et al. 2022). We expect that the combination of vehicle strikes, harvest, and anticoagulant rodenticide-related mortalities together may well put the Adirondack population within that range.

In areas with lower survival, populations may be maintained by increased kit production and recruitment, as well as movement of individuals between populations. Mature female ( $\geq 1$  year old) survival rates for both Tug Hill and Adirondack focal areas were consistent with previous estimates in Maine (0.65, 95% confidence interval [CI] 0.50, 0.96; Paragi et al. 1994) and Ontario (0.63 95% CI 0.47, 0.86 and 0.81 95% CI 0.72, 0.91; Koen et al. 2007). In the Tug Hill focal area, litter sizes necessary to maintain a stable population ( $\lambda = 1$ ; assuming posterior median mature female survival rates) exceeded the number of kits fishers are able to produce (Powell 1993) when  $S_0$  is approximately  $< 0.25$ . In addition to the higher capture rates for fishers  $< 1$  year old in the Tug Hill focal area, we interpret this as evidence for juvenile survival to be on the higher end of the range estimated by Paragi et al. (1994); i.e., closer to 0.50. Further, not all females breed in a given year (Chapter 5; Arthur and Krohn 1991), resulting in lower average litter sizes for the population, and necessitating higher survival. Koen et al. (2007) came to similar conclusions regarding juvenile survival rates for fisher populations in Ontario. Given the higher survival rates of mature females in the Adirondack focal area, juvenile survival may be lower if females are producing the same number of kits across northern New York. Additionally, emigration can have significant impacts on population density and persistence (Hovestadt and Poethke 2006). Genetic analysis of fishers in northeastern North America have indicated that fishers have dispersed from the Adirondack Park to Ontario, Canada (Carr et al. 2007). While we did not directly measure dispersal, we hypothesize that emigration may be

contributing to perceived differences in fisher densities, especially if fishers are traveling further to establish territories with sufficient prey.

We interpret model selection uncertainty with respect to coyote, habitat quality, and stand age impacts on overall survival as indicating that these covariates all describe a similar gradient across northern New York. Additionally, the areas used by the fishers collared for this study were primarily located in regions with higher probability of selection as defined by Jensen and Humphries (2019); the increased mortality here could be an artifact of where fishers are inhabiting rather than a true relationship between habitat quality and survival. Indeed, coyote relative abundance was inversely correlated with stand age ( $r = -0.75$ , 95% CI  $-0.78, -0.72$ ;  $P < 0.001$ ,  $N = 894$ ), and moderately correlated with habitat quality ( $r = 0.60$ , 95% CI  $0.56, 0.64$ ;  $P < 0.001$ ,  $N = 894$ ). Though the resource selection model developed by Jensen and Humphries (2019) indicated fishers avoided areas with coyotes, and risk of mortality tended to increase in areas with greater relative abundance of coyotes, we suspect that, on the broader scale of this study, coyotes may be selecting for similar habitats as fishers. For example, lower habitat quality for fishers identified by Jensen and Humphries (2019) increases with decreasing stand age ( $r < -0.76$ , 95% CI  $-0.78, -0.73$ ;  $P < 0.001$ ,  $N = 894$ ), and coyotes are known to avoid areas with mature forest (Kays et al. 2008). Overlap between coyotes and fisher may be possible without suppression of fisher populations given sufficient alternative prey sources (Heithaus 2001).

While an increase in forest cover has appeared to benefit fisher populations in northeastern North America (Lancaster et al. 2008), and fishers have traditionally been considered specialists of mature or late seral forest types (Buskirk and Powell 1994). However, more recent habitat selection studies indicate that heterogeneous forests, with high structural complexity (Raley et al. 2012), are likely better suited to supporting fisher populations (Sauder



and Rachlow 2015) even more so than so-called ‘pristine’ forests that lack road access (Sauder and Rachlow 2014). We expected that stand age would be associated with lower prey densities, for example, snowshoe hare densities tend to decrease with increasing stand age (Lewis et al. 2011). Thus, we were surprised that the model that included stand age ( $\Delta\text{WAIC} = 0.5$ ) indicated a decrease in mortality risk as stand age increased. However, we consider the possibility of confounding effects among mortality sources and landscape gradients. Indeed, fishers regularly use semi-urban areas surrounding Albany, NY (LaPoint et al. 2013), and nearby Saratoga County sees some of the highest density fisher harvests in the state (NYSDEC unpublished data, New York State Department of Environmental Conservation 2015) despite high suburban development. So, while harvest mortality may be high, it appears that these areas are suitable for producing fishers, as well as protecting them from many sources of non-harvest mortality. In contrast, the fisher population within the central Adirondacks has lower human access and levels of disturbance, resulting in lower overall levels of harvest mortality.

We further had expected that WUI would be associated with an increased risk of mortality, due to increased anticoagulant exposure (Chapter 3), vehicle strikes, and other more general hazards associated with human presence in a landscape. However, within the competing risks framework, we observed lower risk of mortality to both harvest and non-harvest sources as WUI increased, which we quantified within a home-range sized buffer around fisher locations. While the overall range of percent WUI was similar across the two focal areas, the median was overall higher within the Tug Hill where human land uses dominate the landscape. Human land uses in this region act to remove the dominant forest canopy, creating greater habitat heterogeneity (Sonti et al. 2023), and seemingly improving habitat quality for fishers. In addition, areas that are close to dwellings may see lower trapping pressure if trappers are

concerned about domestic dogs being caught in their traps (Triezenberg and Knuth 2018). Therefore, we suggest that for fishers the benefits of using human-dominated landscapes outweigh the risks in this region.

We expected beech mast to have a clear signature on risk of harvest mortality, based on previous work by Jensen et al. (2012) and Greenhorn et al. (2021). Indeed, the risk of mortality increased in mast failure years, especially for harvest mortality. Of the 28 fishers harvested, 20 (83%) of the Tug Hill Plateau fishers and 3 (75%) Adirondack fishers were trapped in mast failure years (2020 and 2022). In contrast, the mast years of 2019 and 2021 saw only 5 fishers harvested across the whole region (4 Tug Hill, 1 Adirondack). While we acknowledge that the trapping season in the Tug Hill focal area was 16 days longer and therefore could have allowed for greater number of individuals taken, no fishers were trapped in December, and only five were harvested in October, leaving the bulk (79%) to be harvested during the same period that trapping was open in the Adirondacks. We interpret the trend in hazard ratio for the effect of mast as evidence for a moderate increase in mortality for non-harvest mortality during mast failure years, supporting mast crops as an important food source for fishers.

Studying fisher survival is a technically non-trivial endeavor. We experienced high rates of censoring due to collar failure or lost radio signals. Based on observations of retrieved collars, it appears that external antennae were easily damaged by the fishers themselves, as were the wires connecting the battery to GPS unit, likely contributing to the high number of individuals censored for being lost to follow-up, a phenomenon observed in other studies (Lewis et al. 2022). We noted similar damage to the GPS loggers that had been affixed to VHF collars. Moreover, it is possible that animals dispersed from our study area, and the difficulty in relocating fishers before they completed their dispersal movements may have been compounded by the short

broadcasting range of VHF signals available on collars small enough to be suitable for fishers. Lastly, we assumed that there was no bias in survival estimates due to commissioning recreational trappers to assist in capturing and releasing rather than harvesting fishers. Of the 81 fishers caught by recreational trappers in this study, only 15 occurred during an open trapping season (5 in TH, 10 in ADK) and all were initial captures rather than recaptures. Indeed, local trappers have assisted in other studies requiring the capture and collaring of fishers (e.g., Koen et al. 2007) and were greatly beneficial to our study.

### **MANAGEMENT IMPLICATIONS**

Our estimates of survival, along with estimates of fisher productivity (Chapter 5), indicate demographic limits to population growth in Adirondack fishers. The uncertainty in model selection that northern New York exhibits a gradient of co-varying conditions that together contribute to variation in fisher survival rates. Wildlife managers are presented with a unique challenge within the Adirondack Park due to the ‘Forever Wild’ clause in the New York State constitution restricting forest management throughout much of the region. While we suspect that food availability is linked to fisher survival rates, managers are unable to alter the habitat to improve prey availability. Thus, management actions may be limited to changes to harvest regulations, at least in the short-term, to improve the long-term sustainability of this species within the Adirondack region.

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## TABLES

**Table 1:** Possible hypotheses for explaining variation in fisher survival across northern New York, 2019–2022. All models included a binary variable for focal area (i.e., Tug Hill Plateau and Adirondack).

Hypothesis	Covariate(s)	Spatial Scale
<b>H0.</b> Fisher survival is not explained by spatial variables	--	
<b>H1.</b> Survival decreases with decreasing habitat quality	RSPF <sup>a</sup>	20 km <sup>2</sup>
<b>H2.</b> Survival decreases in older forests, where prey is less available	Stand age <sup>b</sup>	60 km <sup>2</sup>
<b>H3.</b> Survival decreases with competition with larger carnivores	Coyote <sup>c</sup>	60 km <sup>2</sup>
<b>H3a.</b> The relationship with coyotes may be season-specific, and may benefit fishers when winter conditions favor coyote deer kills (increasing survival where there are more coyotes)	Coyote, WSI	60 km <sup>2</sup>
<b>H3b.</b> Plentiful food in the summer lessens competition between fishers and coyotes, survival expected to be independent of coyote abundance	Coyote	60 km <sup>2</sup>
<b>H4.</b> Survival decreases in mast failure years due to less food, but the effect may be modified by relative habitat quality	Mast year indicator <sup>d</sup> , RSPF	20 km <sup>2</sup>
<b>H5.</b> Survival decreases in mast failure years due to less food, but the effect may be modified forest stand age, which is presumed to have different prey availability	Mast year indicator, Stand age	60 km <sup>2</sup>
<b>H6.</b> Survival decreases in areas heavily modified by human activity and development	WUI <sup>e</sup>	20 km <sup>2</sup>

<sup>a</sup>Resource selection probability function developed by Jensen & Humphries (2019)

<sup>b</sup>Stand age layer derived from Forest Inventory and Analysis data (Wilson et al. 2018)

<sup>c</sup>J. Twining, unpublished model

<sup>d</sup>SUNY ESF Huntington Wildlife Forest

<sup>e</sup>Wildland-urban interface layer developed by Carlson et al. (2022)

**Table 2:** Number of individual fishers captured by sex and age class and focal area across northern New York, 2019–2022. Immature fishers were <2 years old, while adults were  $\geq 2$  years old. The number of individuals included in the risk set is shown in parentheses.

<b>Sex &amp; Age Class</b>	<b>Tug Hill Plateau</b>	<b>Adirondack Park</b>
Immature male	39 (29)	30 (24)
Immature female	42 (35)	22 (17)
Adult male	9 (7)	18 (18)
Adult female	9 (8)	8 (8)
All fishers	99 (79)	78 (67)
Recaptures <sup>a</sup>	4	7

<sup>a</sup>Recaptured individuals were fitted with new collars, and not included in sex and age class totals.

**Table 3:** Comparison of models based on six hypotheses related to fisher survival across northern New York. All models included a binary variable for age group (i.e., adults and immatures). For each model, we include the parameter estimates of the hazard ratio for the effects of age, the spatial layer associated with each hypothesis, the estimated hazard ratio associated with the spatial layer, and the widely applicable information criterion (WAIC) and difference from the lowest WAIC for each model.

<b>Model</b>	<b>Age hazard ratio (95% BCI)</b>	<b>Spatial layer</b>	<b>Hazard ratio (95% BCI)</b>	<b>WAIC</b>	<b><math>\Delta</math>WAIC</b>
H1	1.36 (0.56, 2.87)	Habitat quality	1.47 (0.58, 3.05)	685.0	0
H2	0.56 (0.01, 2.35)	Stand age	0.80 (0.45, 1.36)	685.5	0.5
H3	0.57 (0.01, 2.26)	Coyote relative abundance	1.47 (0.82, 2.40)	686.5	1.5
H0	0.66 (0.01, 2.77)	–	–	686.7	1.7
H6	0.60 (0.01, 2.38)	WUI	0.56 (0.28, 0.96)	697.9	12.9
H5	0.54 (0.01, 2.21)	Mast $\times$ Stand age	1.42 (0.38, 3.79)	745.8	60.8
H4	0.54 (0.01, 2.18)	Mast $\times$ RSPF	1.55 (0.41, 3.97)	746.2	61.2

**Table 4:** Cause-specific mortality of 57 fishers across northern New York State, 2019–2022, excluding individuals that died  $\leq 7$  days from capture.

<b>Mortality Source</b>	<b>Immature Male</b>	<b>Immature Female</b>	<b>Adult Male</b>	<b>Adult Female</b>	<b>Total</b>
Disease (rabies)	0	1	0	0	1
Harvest	7	8	6	7	28
Predation (coyote)	0	1	0	0	1
Rodenticide	0	0	0	1	1
Unknown	4	2	14	2	22
Vehicle Strike	1 <sup>a</sup>	0	2 <sup>a</sup>	1	4

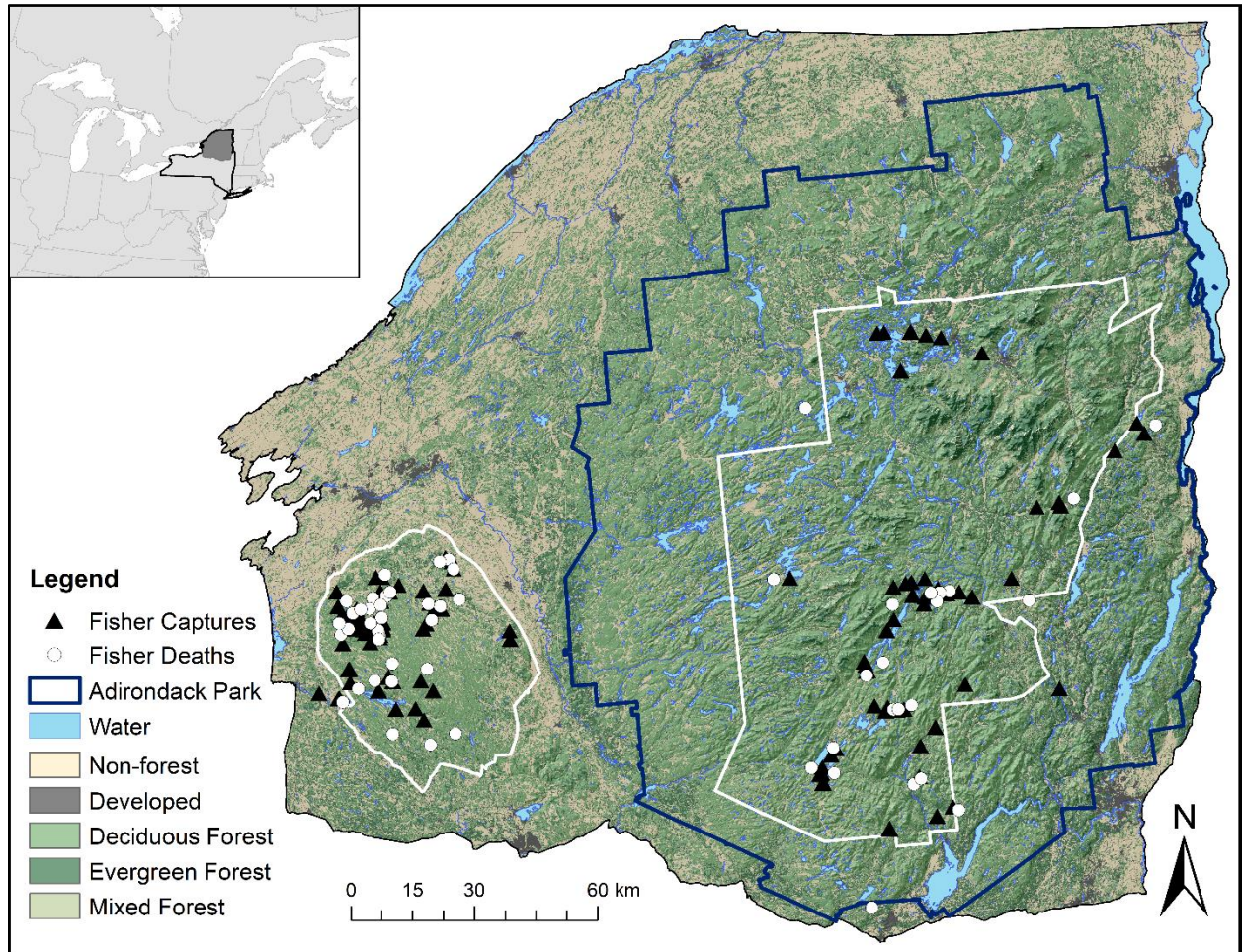
<sup>a</sup>Presumed vehicle strike due to proximity to road and skeletal damage.



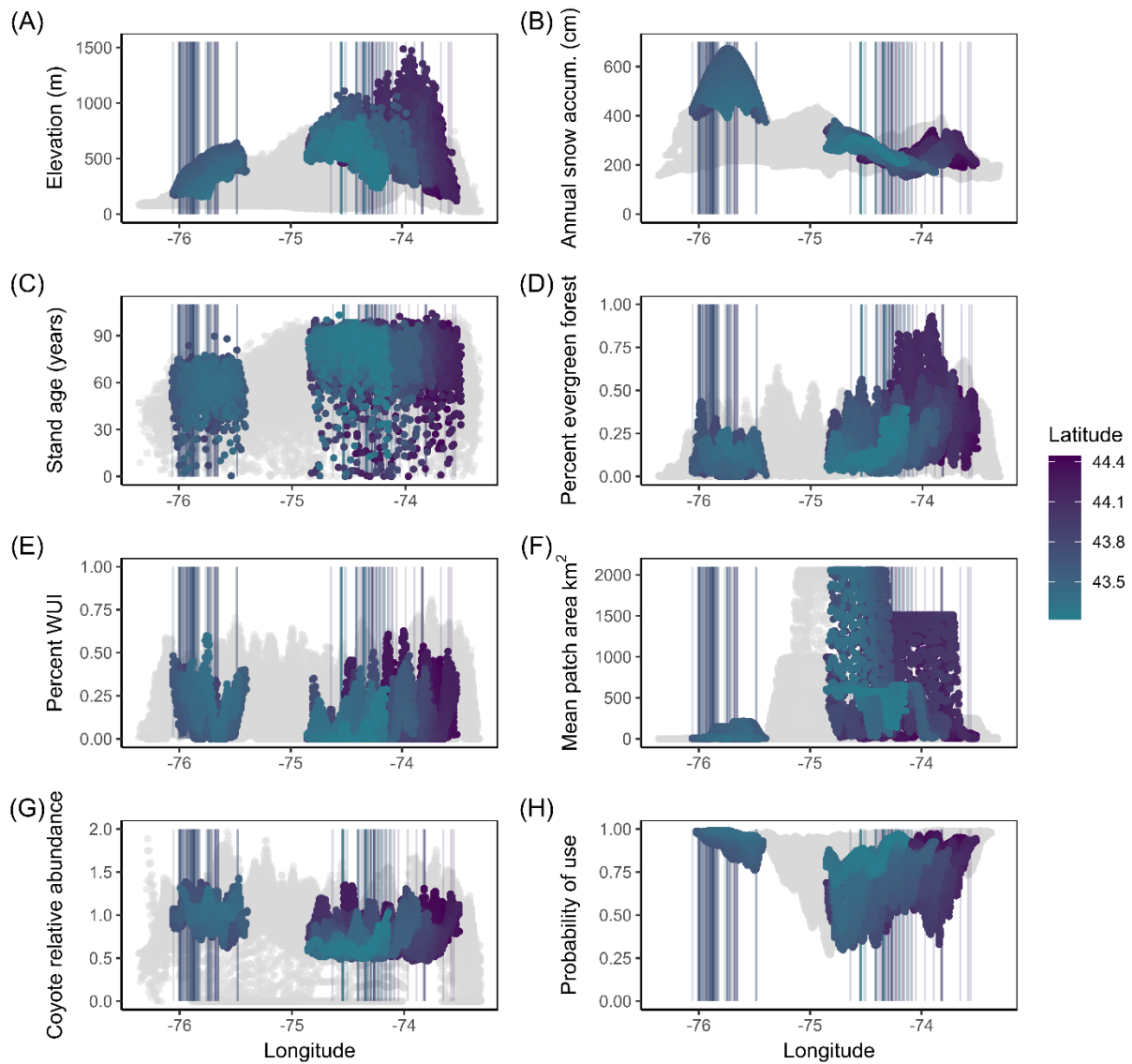
**Table 5:** Number of fishers captured alive per unit effort (100 trap nights) by age group across northern New York, split into focal areas (Tug Hill Plateau [THP] and Adirondack [ADK]), 2019–2022. Juvenile fishers were <1 year old, subadult fishers were  $\geq 1$  year and <2 years old, and adults were  $\geq 2$  years old. For survival analyses, we classified juveniles and subadults together as immatures.

<b>Trapping Season</b>	<b>Juvenile</b>		<b>Subadult</b>		<b>Adult</b>		<b>All individuals</b>	
	<b>THP</b>	<b>ADK</b>	<b>THP</b>	<b>ADK</b>	<b>THP</b>	<b>ADK</b>	<b>THP</b>	<b>ADK</b>
2019	0.08	0.06	0.24	0.06	0.00	0.12	0.32	0.24
2019–2020	0.71	0.15	0.26	0.11	0.19	0.23	1.17	0.48
2020–2021	0.32	0.08	0.11	0.40	0.21	0.18	0.64	0.65
2021–2022	0.40	0.19	0.09	0.36	0.11	0.33	0.60	0.87
All years	0.41	0.13	0.14	0.25	0.15	0.23	0.71	0.61

## FIGURES

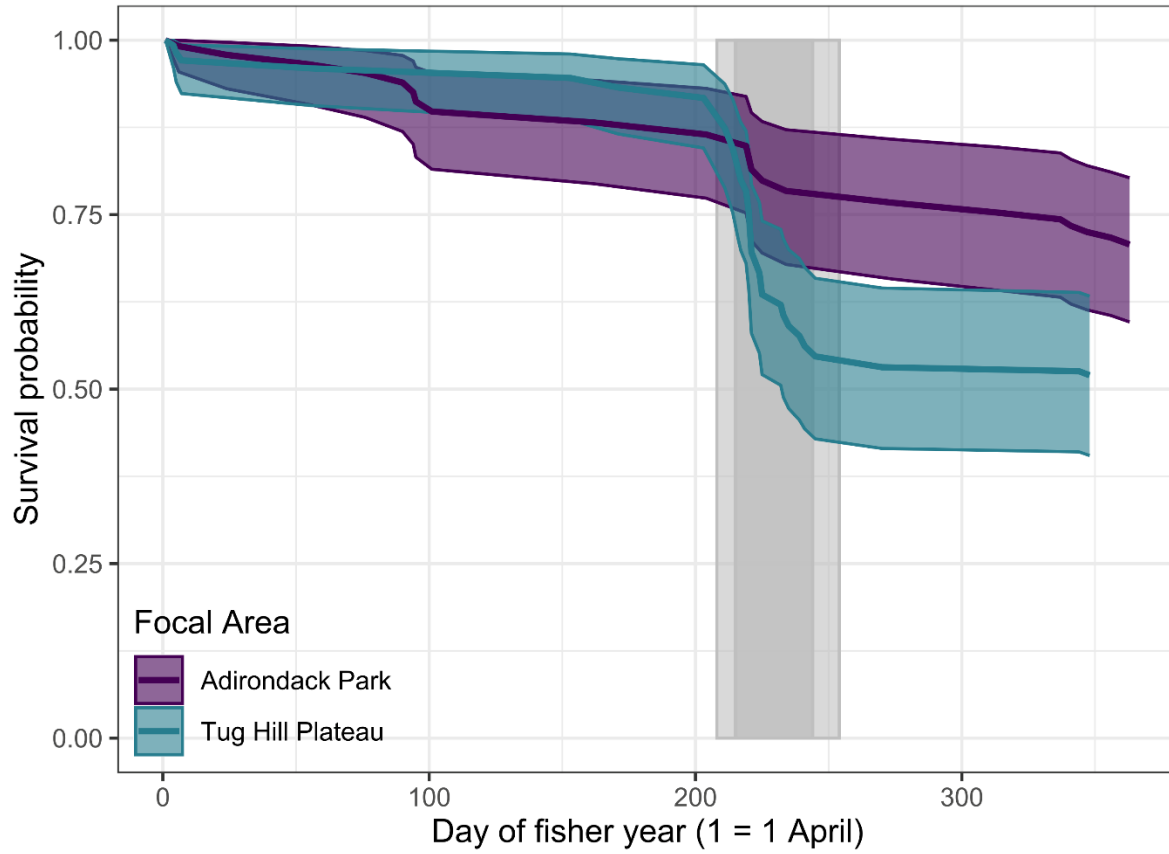


**Figure 1:** Location of fisher captures (black triangles) and deaths (white circles) across northern New York State, USA, 2019–2022. For reference, the Adirondack Park is outlined in dark blue, and focal areas in the Tug Hill Plateau and inner Adirondack Park are outlined in white. Inset shows northern New York (shaded) within New York State (black outline).

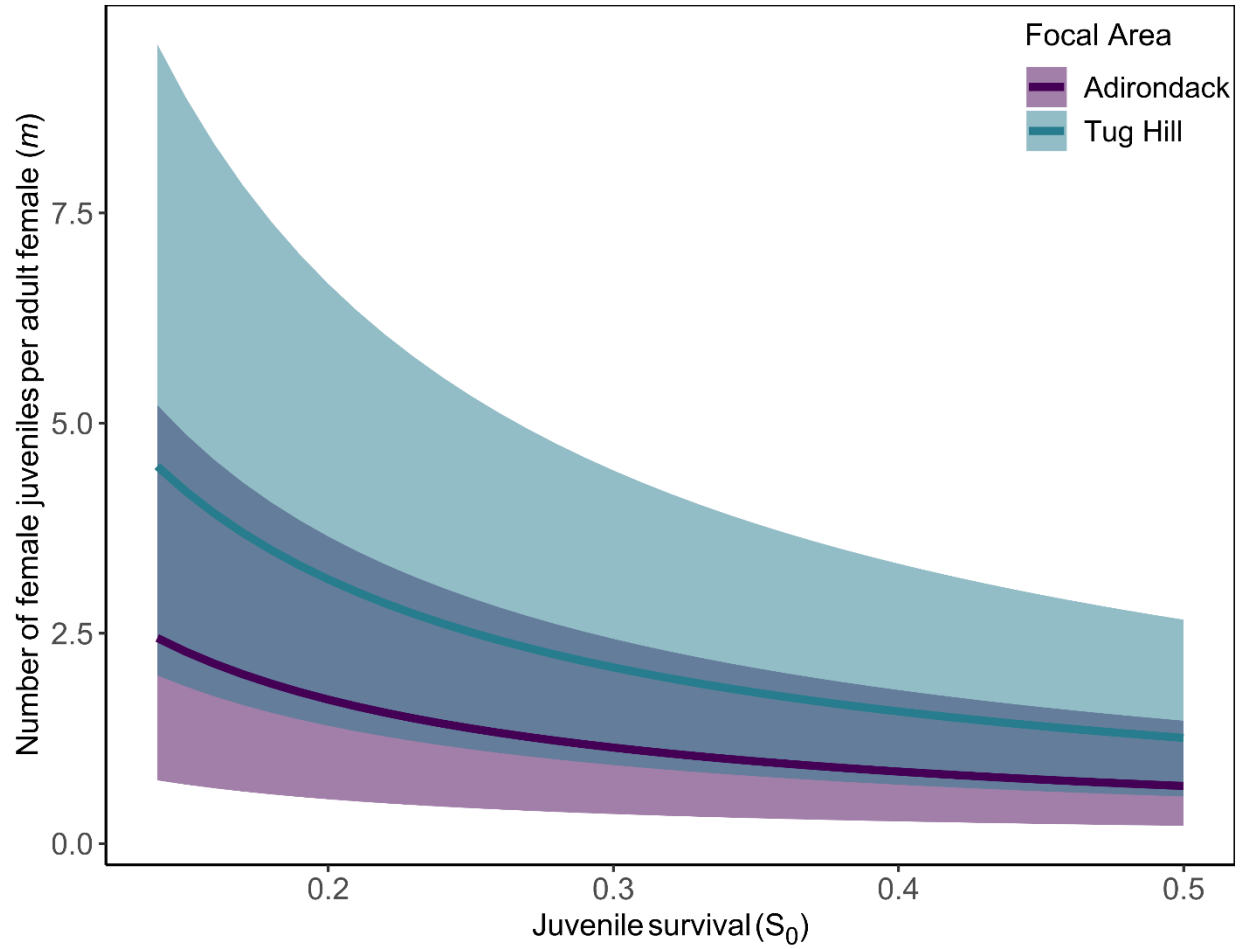


**Figure 2:** Example of landscape gradients across northern New York State across longitude (x-axis) and latitude (point color), including (A) elevation, (B) 15-year average annual snow accumulation between (2008–2023), (C) forest stand age, (D) percentage of  $\sim 25$  km<sup>2</sup> square moving window classified as evergreen forest, (E) percentage of  $\sim 25$  km<sup>2</sup> square moving window classified as wildland-urban interface, (F) average forest patch size using a  $\sim 25$  km<sup>2</sup> square moving window, (G) coyote relative abundance, and (H) probability of fisher used based on a resource selection probability. Gray shadows indicate values over the entirety of northern

New York, while points in color are the values for the two focal areas (Tug Hill Plateau and inner Adirondack Park). Point values for covariates were extracted from a 1×1 km point grid. Vertical lines are located at longitude values where fishers were captured. Note that the sampling area for coyote and probability of use was smaller than the full northern New York.

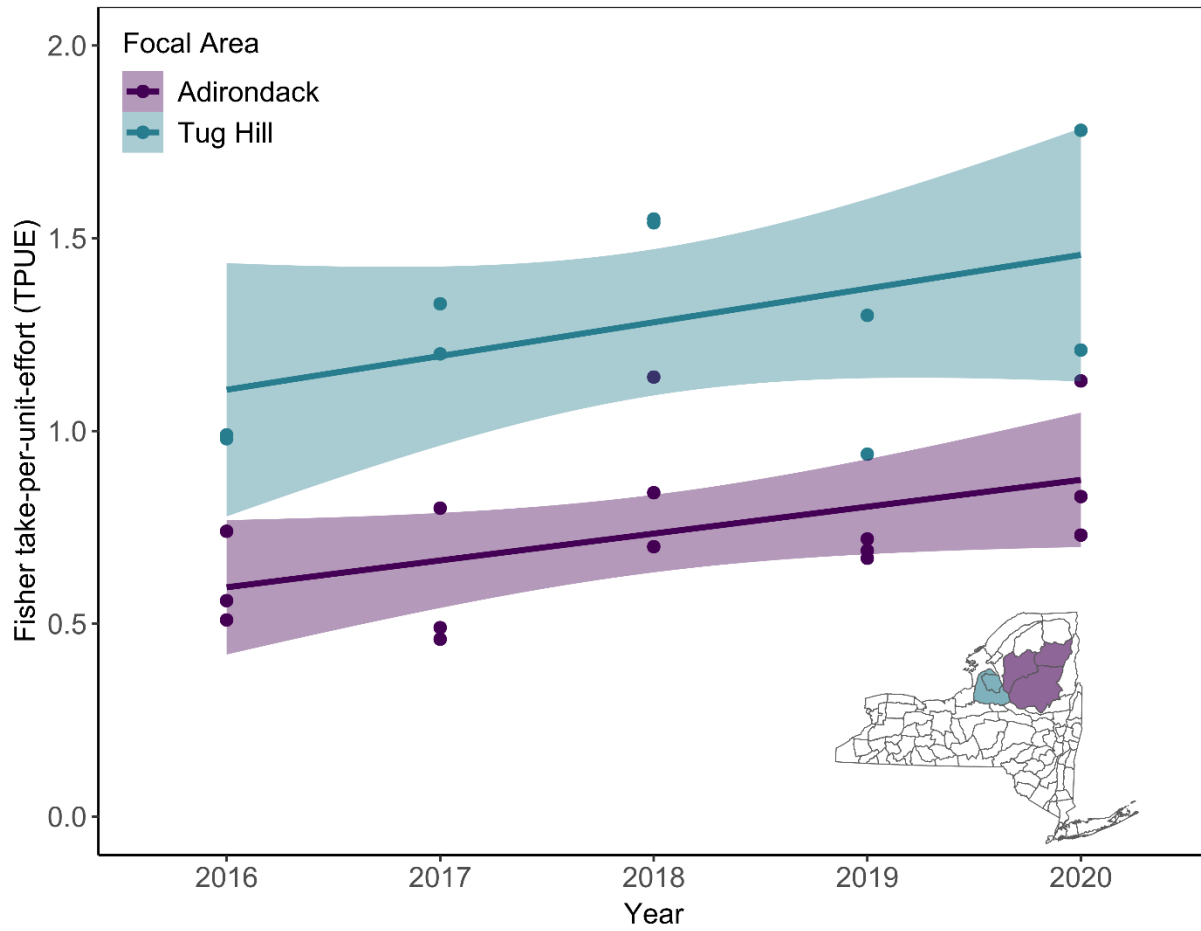


**Figure 3:** Annual (1 Apr–31 Mar) Kaplan-Meier survival curves and 95% Bayesian credible intervals for fishers in two focal areas (Tug Hill Plateau and inner Adirondack Park) in northern New York, USA, 2019–2022. Vertical shading indicates fisher trapping season in the Adirondack Park (dark gray, 1–30 Nov) and Tug Hill Plateau (light gray, 25 Oct–10 Dec) focal areas.



**Figure 4:** Number of female offspring per adult female fisher needed to maintain a stable population across juvenile (<1 year) survival and adult survival based on empirical estimates from Tug Hill Plateau and Adirondack Park focal areas in northern New York, USA, 2019–2022.

#### Appendix 4-1. Fisher TPUE trends



**Figure A1.** Take-per-unit-effort (TPUE) of fishers in northern New York State, 2016–2020, according to wildlife management unit boundaries most closely associated with Tug Hill Plateau and Adirondack Park focal areas.

## **CHAPTER 5: VARIATION IN MATERNAL ATTENDANCE AND FISHER KIT SURVIVAL ACROSS FOREST PRODUCTIVITY AND TEMPERATURE GRADIENTS IN NORTHERN NEW YORK**

### **ABSTRACT**

Recruitment of young individuals into reproductive age classes is an important parameter determining population trajectories. Juvenile survival rates tend to vary markedly given the multifaceted and dynamic factors influencing parental success, such as age, weather, and resource availability. Northern species giving birth in late winter/early spring, such as fishers (*Pekania pennanti*), are especially vulnerable to risks imposed by cold temperatures and deep snows that may mitigate expected variation in recruitment rates across gradients of resource availability. We investigated fisher kit survival from birth to weaning (approximately 10 weeks), and maternal space use and den attendance patterns across the central Adirondack Park, NY and adjacent Tug Hill Plateau – areas that included broad gradients in elevation, landcover, forest composition and structure, and abiotic conditions. Using GPS and accelerometer data from 19 adult female fishers, we quantified home range size, the proportion of each day spent in the den, and the duration of foraging bouts. We related forest stand age, litter size, and minimum temperature to den attendance patterns. Ultimately, we used an extension of the unmarked young survival model to estimate daily kit survival up to 11 weeks old (77 days). Home ranges were larger and more variable within the less productive Adirondack Park landscape. Lower minimum daily temperatures were associated with increases in the proportion of the day spent in the den. Litter sizes ranged 1–4 kits, and kit survival to weaning averaged 0.76 (95% CRI 0.63, 0.86). Daily survival probabilities were driven primarily by forest stand age, with kits exhibiting lower



survival in older forests (i.e., the Adirondack Park), and wildland-interface, with kit survival increasing as the proportion of the surrounding landscape classified as wildland-urban interface increased. Our results indicate that prey abundance and/or availability, determined by forest age class, as well as disturbance from human development, more than harsh spring temperatures was more limiting to reproduction and kit survival across northern New York.

## **INTRODUCTION**

In species with slow-tempo life histories, adult survival rates are generally high and stable, while recruitment—the survival of offspring to the age where they become independent and subsequently join the breeding population—is often much more variable (Gaillard et al. 1998). As a result, juvenile survival has less predictable but no less important impacts on population dynamics compared to adult survival (Finkelstein et al. 2010). On the slower end of the life history continuum species generally produce fewer number of offspring while investing more in parental care (Sæther et al. 2013), with juveniles often completely dependent on one or both parents for a period of weeks to months (Dybala et al. 2013). Because of this, the energetic costs of reproduction, and especially lactation, greatly exceed the energetic requirements of non-reproductive periods (McNab 2006). Where resources are limiting, the cost of reproduction generally comes in the form of decreased maternal condition or survival (Toni et al. 2020).

In order to support themselves and offspring, females must forage efficiently (i.e., intake energy that exceeds the energy expended to capture prey; Powell and Leonard 1983, Jeanniard-du-Dot et al. 2017). Thus, habitat choices underlie the demographic rates that drive population growth (Morris 2003). Ideally, animals select habitats that have the highest quality and will yield the greatest fitness benefits (Fretwell 1972), with females expected to maintain a home range

only as large as necessary to meet energetic requirements for their own maintenance and provisioning of offspring (Sandell 1989, Arthur and Krohn 1991, Katnik et al. 1994). Home range size will likely increase, and population density decrease, where prey distribution is less predictable and prey density is low (Clutton-Brock and Harvey 1978), such as in highly seasonal or unpredictable environments (Herfindal et al. 2005)—as observed in grizzly bears (*Ursus arctos*; Edwards et al. 2013), black-footed ferrets (*Mustela nigripes*; Jachowski et al. 2010), and other taxa (Fuller and Sievert 2001). Thus, availability and predictability of prey, including the effort required to obtain it, is linked tightly to reproductive potential (McNab 2006).

Maternal age, condition, and experience likely play a role in mitigating costs of reproduction (Descamps et al. 2009) and contributing to variation in reproductive success (Côté and Festa-Bianchet 2001). Females in good condition may be better able to cope with sparse resource availability than those in poor condition (Hertel et al. 2018, Badger et al. 2020). As individuals age, they may increase their foraging success and efficiency (Daunt et al. 2007), gain a better appreciation of the risks facing unsupervised young (Erlandsson et al. 2017), or secure access to better resources after previously being aggressively excluded from such areas by more dominant individuals (Fretwell and Lucas 1970). Because higher-ranking mothers will likely have access to higher resource quality or quantity, dependent juvenile survival is often density dependent (Hurley et al. 2020). Further, the effects of density may interact with weather conditions (Portier et al. 1998), which may directly influence juvenile survival (Robinson et al. 2007) or limit maternal access to food (Neuhaus et al. 1999). Therefore, species that give birth when conditions are less favorable in late winter/early spring face several challenges in raising young (Linton and Macdonald 2018).

Fishers (*Pekania pennanti*) are forest-dwelling mustelids that give birth from early March to early April (Frost et al. 1997, Powell et al. 2003, Facka et al. 2016) and use tree cavities to raise their young (Powell 1993). Fisher kits are reared in 1–5 reproductive dens for approximately ten weeks (Paragi et al. 1996). This period of vulnerability is a critical life history stage for fishers, with kit survival hypothesized to be more limiting than kit productivity (Jensen and Humphries 2019). Litter mortality prior to weaning has been estimated to be up to 60% in fishers (Matthews et al. 2013, 2019, Green et al. 2018), though individual kit mortality is likely even greater (Matthews et al. 2019). Threats to kit survival include exposure to harsh temperatures, malnutrition due to low prey density, predation of the mother (Green 2017, Matthews et al. 2019), and predation by males (Matthews et al. 2019, Smith et al. 2020). Powell (1993) suggested that female fishers are more frequently active when they have kits in a den, while their movements are also more restricted (i.e., a female is limited in how far she can range to find prey and cannot go as long between meals). Meeting energetic needs under those constraints is made even more challenging given the unpredictability of late winter and early spring conditions controlling food availability (Jensen and Humphries 2019).

We sought to determine spatial differences in fisher maternal attendance and kit survival across a study area spanning from the central Adirondacks westward to the more productive Tug Hill Plateau. Harvested data from 2005–2013 indicated a potential decline in fisher abundance within the Adirondack Park, NY (New York State Department of Environmental Conservation 2015), so we expected to see regional differences in demographic rates. Our objectives were to (1) quantify regional differences in home range size and den attendance patterns and relate those differences to environmental gradients, and (2) estimate kit survival throughout the denning period—the period between birth and when they become independently mobile. We

hypothesized that northern New York contained a gradient of environmental conditions that would result in differences in fisher kit survival; for example, while the Adirondack Park contains vast, undisturbed wilderness, the Tug Hill Plateau exhibits greater variability in forest management practices, lies in close proximity to agriculture and human development, and likely yields greater prey diversity and relative abundance despite a presumed increase in risk of toxicant exposure (Chapter 3). Additionally, differences in elevation influence variability in abiotic conditions that influence spring vegetation growth, productivity, and thermoregulation requirements of mammals (Jensen and Humphries 2019). Therefore, we predicted that fishers further east (Adirondack Park) would spend more time outside of the den, maintain larger home ranges, make longer movements for foraging bouts, and see decreased kit survival compared to fishers further west (Tug Hill Plateau).

## **METHODS**

### ***Study area and fisher captures***

We focused our work within the Adirondack Park (75° 44' 16.188" W, 43° 37' 53.51" N) and the nearby Tug Hill Plateau Hill (74° 15' 20.988" W, 43° 52' 51.49" N). Northern New York lies within the temperate-boreal ecotone (Evans and Brown 2017), dominated by northern hardwood and mixed conifer tree species. The approximately 24,000 km<sup>2</sup> Adirondack Park contains several small towns but much of the forest is protected from management or development. The similarly forest-dominated Tug Hill Plateau lies to the west of the Adirondack Park, contains more heterogeneous forest conditions due to active forest management, and is surrounded by agriculture and urban centers. Weather conditions are similar across the region, the Tug Hill Plateau experiences a greater frequency of heavy snow events due to its location directly east of

Lake Ontario (Scott and Huff 1996, Veals and Steenburgh 2015). Spring is generally wet and cool across the state. Elevation in our focal area ranged from 200–1600 m above sea level, with an eastward gradient towards more extreme terrain conditions and by extension lower daily temperatures.

Our trapping season ran from 25 October–8 March each year 2019-22. Fisher capture and handling protocols were approved by the SUNY ESF Institutional Care and Use Committee (protocol #190902) and under permit of New York State Department of Environmental Conservation, with trapping details provided in Cunningham et al. (2022). We anesthetized fishers, extracted a tooth (PM1) for cementum annuli aging by Matson’s Laboratory (Manhattan, MT, USA), and drew blood from the jugular vein to measure progesterone in females at the Cornell Wildlife Health Laboratory. We estimated age of female fishers via tooth wear and nipple size (Paragi 1990, Frost et al. 1999) and considered females to be adults at  $\geq 1.5$  years old, as females can produce their first litter at 2 years old (Powell 1993). We fit juvenile females with VHF collars (Advanced Telemetry Systems, Isanti, MN, USA) and adult females with Lotek LiteTrack RF 40 GPS/VHF collars with SWIFT fixes enabled (Lotek Wireless, Newmarket, ON, Canada). GPS collars collected 8 fixes/day between 20 Feb and 31 May, and 2 fixes/day the rest of the year. The collars were equipped with temperature sensors and accelerometers that summarized activity over 5-minute intervals between 1 March and 31 July.

### ***Den monitoring and kit observations***

To locate reproductive dens, we tracked adult female fishers beginning mid-March via aerial and ground telemetry. In addition to females that received GPS collars, we monitored females that were fitted with VHF collars as juveniles in previous trapping seasons. We attempted to locate

female fishers 2–3 times/week. When a given female was found in the same tree on  $\geq 2$  consecutive occasions (Paragi et al. 1996, Green et al. 2017), we set out 2–6 Reconyx PC800 or Hyperfire 2 Covert (Reconyx Inc, Holmen, WI, USA) or Browning Spec Ops BTC8 (Browning Trail Cameras, Birmingham, AL, USA) camera traps trained on the tree. We checked cameras every 2–10 days and initiated a search for a new den tree after observing photos of the female moving kits away from the den. Occasionally, we misidentified a rest site as a den, and moved the cameras after we failed to detect a fisher at the site for several consecutive days. We noted changes in activity patterns that could be indicative of litter loss (e.g., failure to identify a structure being used regularly for several weeks). We attempted to download GPS and acceleration data whenever the female was located in a den and continued to relocate her at least once per week after kits were weaned and moving on their own.

We processed photos collected at dens following the procedures outlined in Cunningham et al. (2022), assigning tags to photo metadata with digiKam software (version 7.7.0, [www.digikam.org](http://www.digikam.org), accessed 10 August 2022) and using the *exifr* v. 0.3.2 (Dunnington and Harvey 2021) and *camtrapR* v. 2.2.0 packages (Niedballa et al. 2016) to import photo metadata into R (R Core Team 2023). All photos tagged as having a kit in them were confirmed by S. Cunningham who also recorded mode of movement (i.e., kits carried or under their own power). During each den transfer we counted the number of kits moved by each female, using photo timestamps to differentiate the transfer of individual kits as well as temporary movements (i.e., mom carrying a kit out and then back in or exploratory movements by kits) versus den relocation.

We estimated parturition date based on multiple lines of evidence from GPS and accelerometer data (Hooven et al. 2022). Decreased travel distances and clustered locations are

often indicative of reproductive behavior (e.g., DeMars et al. 2013, Asher et al. 2014, Peterson et al. 2018), and accelerometers are being more frequently used to identify birth or hatch events across a variety of species (e.g., Clarke et al. 2021, Marchand et al. 2021, Schreven et al. 2021). We combined accelerometer data into a single ‘activity’ metric for each 5-minute interval by taking the square root of the summed squared values of both activity axes, similar to the vectorial sum of the overall dynamic body acceleration described by Qasem et al. (2012). We calculated a rolling average of activity with a window of 12 (1 hour) using the *zoo* package v. 1.8-12 (Zeileis and Grothendieck 2005) in R (R Core Team 2023). We performed k-means clustering using activity, rolling mean of activity, and temperature (measured by the collar) to classify periods of rest versus activity. To further refine our classifications, we used run length encoding to quantify the number of consecutive class labels, and swapped the label for any segments <1-hr long, as these were assumed to be short rest periods, based on a companion study comparing activity as observed by collars versus trail cameras (Cunningham et al. 2022). After classifying accelerometer data into active or rest periods, we extracted two metrics to indicate potential parturition dates: (1) The day showing the lowest overall activity (i.e., summed activity values over a 24-hour period), and (2) the midpoint (day) of the longest continuous period of resting data.

Next, we examined fix success for each female throughout March. Because terrain and vegetation cover can influence the probability of collars obtaining a GPS fix (Ironside et al. 2017, Hofman et al. 2019), it follows that time spent in tree or underground dens would reduce fix success. Thus, we expected low fix success on the date of parturition when the female spends the majority of time in the den as has been observed with brown hyenas (*Parahyena brunea*; Wiesel et al. 2019). We again used run length encoding to quantify the longest segment of

consecutive missed fixes and used the date at the beginning of the segment as the estimated day of parturition. We looked for alignment in at least two of the three measurements (minimum daily activity, longest in-den period, and longest segment of missed GPS fixes), and compared the estimated dates to the dates when cameras were first set for each female fisher (Table 1). In some cases, the three metrics indicated a discrepancy of  $\leq 3$  days, for which we took the median as the day of parturition. For females fitted with VHF-only collars, we assigned the mean parturition date based on GPS-collared females in each study region and year and compared mean values to field data to ensure relative alignment with denning activity.

### ***Environmental covariates***

We quantified covariates representing abiotic conditions and prey availability thought to influence kit survival. To quantify risk due to exposure, we used daily minimum temperature data from DAYMET (Thornton et al. 2020). We used the *terra* package v. 1.4-22 (Hijmans 2021) to extract minimum temperatures for each day for each fisher at the center of their den-use area (i.e., averaged coordinates of all observed den trees). We used a modeled stand age layer (30 m resolution) created by US Forest Service researchers from Forest Inventory and Analysis and Landsat data (Wilson et al. 2018) as a proxy for landscape productivity, and by extension, prey availability. We also used a 30-m resolution wildland-urban interface (WUI) layer (Carlson et al. 2022), which classifies each pixel as WUI when building density (Bing Maps Team 2018) within a 250 m radius exceeds 6.17 units/km<sup>2</sup> and contains >50% wildland vegetation (i.e., forest, shrub/scrub, grassland, and wetlands), or if the pixel is within 2.4 km of  $\geq 5$ -km<sup>2</sup> block of vegetation (Bar-Massada et al. 2013). We calculated the average stand age and proportion of intermix within a 15-km<sup>2</sup> buffer around the center of the den-use area (hereafter denning



centroid) using the *exactextractr* package (Baston 2022). We selected 15 km<sup>2</sup> to reflect previous estimates of fisher home range size (Fuller et al. 2016). We centered and scaled covariates to have mean of 0 and standard deviation equal to one 1 and checked for collinearity via correlation coefficients. We checked for problematic collinearity via correlation coefficients and did not include variables in the same model when  $r > |0.7|$  (Dormann et al. 2013).

### ***Maternal attendance patterns***

We examined the female's den attendance patterns during the denning period, which was defined as birth until the day before kits were first observed crawling or climbing outside of the den under their own power. We considered multiple levels of temporal scaling (McCann et al. 2017) to quantify maternal attendance patterns. We used accelerometer data to investigate the proportion of each day a female fisher spent in the den and the duration of individual foraging bouts. We investigated space use at a broader temporal scale via denning period home range estimates. For the analyses to follow, we pooled individuals across years due to low sample sizes.

We modeled the effect of stand age, number of kits, daily minimum temperature, and the interaction between minimum temperature and day on the proportion of a day each female spent in the den. We considered all periods away from the den, based on activity classifications of 'active,' that exceeded 10 minutes to be 'foraging bouts' given similarities in energy expenditure with other activities, such as mating (Powell and Leonard 1983). We used a binomial GLMM with a logit link to model the number of activity periods classified as in the den out of the total number of 5-minute activity periods in a day ( $n = 288$ ). Temperatures generally increased throughout the denning period as winter transitioned into spring and summer, and after detrending temperature we retained residuals for daily minimum temperature using the *lme4*

package *v. 1.1-33* (Bates et al. 2015). Next, we modeled the effect of average distance from the den and stand age on the duration of a foraging bout (in hours). We subset the full set of foraging bouts to periods when we were observing dens with camera traps to ensure we had a starting location for each GPS fix. We filtered the GPS data to foraging bouts. For each location, we extracted the average stand age within a 100-m buffer and calculated the distance between each location and the den. We then averaged stand age and distance to the den within each foraging bout. Visual inspection of the data indicated that bout duration was not normally distributed; therefore, we used the *fitdistrplus* package *v. 1.1-11* (Delignette-Muller and Dutang 2015, Delignette-Muller et al. 2015) to determine an appropriate distribution, and modeled bout duration as a gamma random variable (Appendix 5-1).

In models for proportion of time in the den and bout duration, we included a random intercept for individual due to repeated measurements for each, and a fixed effect for day to account for temporal autocorrelation. We used normal priors for the mean intercept of the random effect with mean 0 and variance 1,000, and uniform priors constrained between 0 and 100 for the standard deviation of the random intercepts. We used normal priors with means of 0 and variances equal to 100 for regression coefficients for the bout duration model. In the model for the proportion of the day spent in the den, we used priors mean of 0 and variance of  $1.5^2$  for regression coefficients (Northrup and Gerber 2018). For the shape parameter in the bout duration model, we used a uniform distribution ranging from 0 to 100.

We estimated home ranges for each GPS-collared female via autocorrelated kernel density estimation (AKDE; Fleming et al. 2015) using the *ctmm* package *v. 1.1.0* (Calabrese et al. 2016, Fleming and Calabrese 2022) in R (R Core Team 2023), and followed the procedures described by Calabrese et al. (2016) for model selection. We incorporated weights to mitigate the

effects of missed locations (Fleming et al. 2018). We filtered GPS locations used in estimating home ranges to limit the estimates to the known denning period for each female (e.g., estimated parturition to observations of kits moving independently). We compared 95% AKDE home range sizes between east (Adirondack) and west (Tug Hill Plateau) regions of the study area using a t-test for unequal variances. We log-transformed home range estimates to constrain the model to values  $\geq 0$ . We used normal priors for study region means, with a mean of 0 and variance of 1,000, and uniform distributions 0–1000 for the study region standard deviations.

### ***Kit survival***

We modeled kit survival throughout the denning period, which we fixed to 77 days (11 weeks). Recently, Bayesian implementations of the unmarked young survival model (Lukacs et al. 2004) have estimated survival via  $N$ -mixture models and their extensions (Williams et al. 2020), including abundance models for open populations (Dail and Madsen 2011). We based our model on one such implementation developed by Street et al. (2022), where daily survival was estimated based on periodic counts of unmarked offspring. For female  $i$  moving kits on day since parturition  $t$ , we considered counts of kits  $c_{i,t}$  to be a random variable following a binomial distribution with parameters  $p$ , the probability of observing individual kits, and  $N_{i,t}$ , the true number of kits alive for each adult female:

$$c_{i,t} \sim \text{Binomial}(p, N_{i,t})$$

We were concerned about potential disturbance of denning fishers, and therefore were unable to obtain initial litter sizes, so we estimated litter size probabilistically within our model. Because mammalian litter sizes are often under-dispersed relative to a traditional Poisson distribution (Lynch et al. 2014), we used a Conway-Maxwell Poisson distribution to probabilistically

estimate initial litter size. The Conway-Maxwell Poisson distribution is defined by the mean  $\lambda$  and dispersion parameter  $\nu$ , where  $\nu > 1$  indicates under-dispersion (Lynch et al. 2014).

Therefore, we estimated true number of kits for each female fisher  $i$  on day  $t = 1$  (day of birth) as

$$N_{i,1} \sim \text{Conway-Maxwell Poisson}(\lambda, \nu)$$

To ensure the estimated values would not be less than the maximum count of observed kits, we supplied initial values to the model that automatically truncated the distribution for  $N_{i,1}$  to be at least as large as the maximum count for a given female. After day  $t = 1$ , the true number of kits was represented by:

$$N_{i,t} \sim \text{Binomial}(N_{i,t-1}, \phi_{i,t-1})$$

where  $\phi_{i,t-1}$  was apparent survival probability for kits of female fisher  $i$  on day  $t - 1$ , though in this case apparent survival is likely equal to true survival (Lukacs et al. 2004) as fisher kits are dependent on their mother until late summer or early autumn (Arthur and Krohn 1991, Powell 1993, Sweitzer et al. 2015). Because kit survival is conditional on survival of the mother, we configured the model to move to the next individual before the end of the 11-week period if we observed the death of a female. Additionally, we were able to infer the complete loss of a litter based on maternal behavior (e.g., unable to locate a structure being used regularly), and filled the data matrix with zeroes after this point.

We investigated the effects of maternal and environmental covariates on daily survival rates:

$$\begin{aligned} \text{logit}(\phi_{i,t-1}) = & \alpha + \beta_1 \times \text{age}_i + \beta_2 \times \text{freeze}_i \\ & + \beta_3 \times \text{stand}_i + \beta_4 \times \text{WUI}_i \end{aligned}$$

where  $age_i$  was the age of each adult female,  $freeze_i$  indicated the number of days during the denning period ( $n = 77$  days) where minimum temperature was  $<0^\circ\text{C}$ ,  $stand_i$  was the average stand age in years within a 15-km<sup>2</sup> buffer of the central denning area (i.e., centroid of identified dens for individual  $i$ ), and  $WUI_i$  was the proportion of the 15-km<sup>2</sup> buffer classified as wildland-urban interface (correlation coefficients are shown in Appendix 5-2). Because all covariates were indexed by adult female fisher  $i$ , daily survival rates were constrained to be constant throughout the denning period. Thus, we converted between daily survival  $\phi_{i,t}$  and den period survival  $\phi_i$  by raising  $\phi_{i,t}$  to the  $n^{\text{th}}$  power, where  $n$  was equal to the number of days in the denning period, fixed to 77 days to accommodate the longest period between estimated parturition and last observed den moves. We performed a basic validation simulation (DiRenzo et al. 2023) of our model by simulating a single new dataset from the posterior means of model parameters and comparing overlap of posterior densities between the simulated and original data.

In this model, the  $\lambda$ ,  $\nu$ ,  $\mu$ ,  $\beta_{1-4}$  and  $p$  parameters required prior distributions. We used uniform distributions for  $\lambda$ ,  $\nu$  and  $p$ . Mean litter size was constrained between 1.5 and 4, based on observed litter sizes for fishers (Green et al. 2018). Similarly, we used a range of 1–2 for the dispersion parameter  $\nu$ , expecting that litter sizes larger than 4–5 would be rare. We expected detection probability to be high based on preliminary investigations of detection probability (Cunningham et al. 2022), so we constrained the prior for  $p$  to be between 0.9 and 1. Regression coefficients (intercept  $\mu$  and effect  $\beta$ ) had normal priors with a mean of 0 variance equal to 1.5<sup>2</sup> (Northrup and Gerber 2018).

### ***Model implementation***

We fit maternal attendance and kit survival models using the *nimble* package v. 1.0.1 (de Valpine et al. 2017, 2022) in R v. 4.3.1 (R Core Team 2023). We used the *COMPoissonReg* package v. 0.8.0 (Sellers et al. 2022) to generate values for the Conway-Maxwell Poisson random variable. In all models, we sampled from 3 MCMC chains without thinning. For proportion of day in den models we ran 30,000 iterations burning in the first 15,000, for bout duration models we ran 25,000 iterations and burned in 14,000, for home range models we fit 5,000 iterations and burned in 2,500 iterations, and for kit survival models we ran 25,000 iterations and burned in 10,000. We assessed model convergence via visual inspection of traceplots and  $\hat{R}$ , calculated via the *MCMCvis* package v. 0.16.0 (Youngflesh 2018), considering convergence to be achieved when  $\hat{R} < 1.05$ . We considered regression coefficients to be impactful if the proportion of posterior samples greater or less than zero ( $F$ ) exceeded 0.95.

### **RESULTS**

We collared 81 female fishers during our study period (recapturing 7), with 44 determined (via cementum annuli aging) or estimated to be sexually mature in the upcoming denning season. We monitored 19 breeding female fishers (10 in the Tug Hill and 9 in the Adirondack study areas) aged 2–5 years. The proportion of collared female fishers observed with kits varied across years but ranged from 0–0.77 (Table 2). From our sample of 19 productive females, we monitored 78 dens and obtained kit counts at 62, with 47 of those being occasions where the female carried kits to a new den. Estimated parturition dates ranged from 14 March–9 April, with an average of 25 March (Table 1).

### ***Proportion of day spent in den***

Our results indicated strong temporal trends in the proportion of time female fishers spent in the den. The proportion of time female fishers spent in their dens decreased with days since parturition ( $\hat{\beta}_3 = -0.50$ , 95% CRI  $-0.51, -0.49$ ;  $F = 1$ ; Figure 1), with predicted averages of 75% of the day in the den on the day of parturition and 36% of the day in the den on day 77. The interaction between temperature and day was not impactful ( $\hat{\beta}_5 = -0.003$ , 95% Bayesian credible interval  $0-0.01, 0.003$ ;  $F = 0.83$ ). Fishers also spent less of the day in the den when temperatures were warmer ( $\hat{\beta}_1 = -0.01$ , 95% CRI  $-0.02, -0.001$ ;  $F = 1$ ), though the overall effect size was small. Fishers with more kits spent more time in the den ( $\hat{\beta}_2 = 0.05$ , 95% CRI  $0.02, 0.07$ ;  $F = 1$ ), as did those in areas with older forest stands ( $\hat{\beta}_4 = 0.04$ , 95% CRI  $0.02, 0.05$ ;  $F = 1$ ). However, the difference in forest stands of 37 years old saw a predicted average of 54% of the day in the den, whereas fishers in forests averaging 95 years old were predicted to spend an average of 59% of the day in the den.

### ***Foraging bout duration***

Average bout duration was similar between focal areas but slightly higher in the Adirondack Park ( $\bar{x} = 5.1$  hr,  $\sigma = 3.2$  hr) than the Tug Hill Plateau ( $\bar{x} = 4.4$  hr,  $\sigma = 2.9$  hr). Bout duration increased with the average distance from the den ( $\hat{\beta}_1 = 0.13$ , 95% CRI  $0.07, 0.19$ ;  $F = 1$ ; Figure 3). The model predicted an average bout duration of 4.5 hours with an average distance of 0.5 km from the den, and 7.3 hours when the average distance from the den was 3 km. Stand age was not a strong predictor of bout duration, though trended slightly negative ( $\hat{\beta}_2 = -0.05$ , 95% CRI  $-0.14, 0.03$ ;  $F = 0.90$ ), opposite of our expectations. Coincident with the decline in time spent in

den, bout duration showed an increasing trend with days since parturition ( $\hat{\beta}_3 = 0.02$ , 95% CRI – 0.03, 0.72;  $F = 0.75$ ), but not with high confidence.

### ***Home range size***

We observed nearly an order of magnitude difference between the largest and smallest home range during the denning season. The 95% AKDE for 13 females with GPS collars ranged from 2.9 km<sup>2</sup> (95% confidence interval [CI]: 2.5–3.4 km<sup>2</sup>) to 22.0 km<sup>2</sup> (95% CI: 18.1–26.3 km<sup>2</sup>; Figure 3), averaging 7.3 km<sup>2</sup> (95% CI: 6.2–8.6 km<sup>2</sup>). The estimated mean home range for fishers in the Tug Hill Plateau region ( $\hat{\mu}_1 = 5.17$  km<sup>2</sup>, 95% Bayesian credible interval [CRI] 3.89, 6.99; N = 8) was only slightly smaller than estimated mean home range for fishers further east in the Adirondack Park ( $\hat{\mu}_2 = 8.72$  km<sup>2</sup>, 95% CRI 2.86, 25.05; N = 5), with substantial overlap in the posterior distributions between regions.

### ***Kit survival***

The maximum observed litter size ranged from 1–4 kits ( $\bar{x} = 2.42$ ,  $\sigma = 0.90$ ). Average litter size was slightly higher and more variable in Tug Hill fishers ( $\bar{x} = 2.70$ ,  $\sigma = 0.94$ ) than Adirondack fishers ( $\bar{x} = 2.11$ ,  $\sigma = 0.78$ ). We obtained an average of 2.42 counts, or follow-up observations, per litter (Table 1), and while study-area specific means were similar we achieved, for unknown reasons, less variation in counts for Tug Hill ( $\bar{x} = 2.40$ ,  $\sigma = 0.70$ ) versus Adirondack fishers ( $\bar{x} = 2.44$ ,  $\sigma = 1.42$ ). We assumed the loss of two litters; one due to death of the mother and the other due to behavioral patterns indicating the female lost or abandoned her litter. One female dropped her collar at the base of her first den tree, preventing us from relocating her and determining the fate of her litter, but we were able to include one count for her in the model. The mean estimated



initial litter size ( $\hat{\lambda}$ ) was 3.40 kits (95% CRI 2.37, 3.50), and the dispersion parameter ( $\hat{\nu}$ ) was 1.43 (95% CRI 1.07, 1.82). Overall, kits were detected with a probability of 0.94 (95% CRI 0.91, 0.98). The average probability of kit survival for the denning period was 0.76 (95% CRI 0.63, 0.86), and ranged from 0.15 (95% CRI 0.001, 0.56) to 0.99 (95% CRI 0.94, 1.00). We did not detect an effect of maternal age ( $\hat{\beta}_1 = 0.05$ , 95% CRI  $-0.94$ , 1.08;  $F = 0.53$ ) nor the number of freeze days ( $\hat{\beta}_2 = -0.23$ , 95% CRI  $-1.20$ , 0.78;  $F = 0.68$ ) on kit survival. However, stand age ( $\hat{\beta}_3 = -1.05$ , 95% CRI  $-2.11$ ,  $-0.14$ ;  $F = 0.99$ ) and WUI ( $\hat{\beta}_4 = 0.98$ , 95% CRI 0.04, 2.15;  $F = 0.98$ ) proved impactful. Estimated denning period survival rate decreased as stand age increased (Figure 4a), and increased as proportion of WUI increased (Figure 4b). Average stand age within 15-km<sup>2</sup> buffers around den centers ranged 52.5–81.5 and, over this range, predicted daily survival probabilities from 0.9996 (95% CRI 0.9977, 1.0) to 0.9908 (95% CRI 0.9659, 0.9983; Figure 4c), which translates to predicted den period survival rates of 0.97 and 0.50, respectively. Stand age tended to increase from west to east, while den period survival appeared to decrease, and become increasingly variable, over this span. Similarly, the proportion of WUI tended to be higher in the west and lower in the east (Figure 4d), with predicted den period survival ranging from 0.67 in areas without WUI, to 0.99 in areas with 50% WUI in a 15 km<sup>2</sup> buffer. The posterior distributions from the validation simulation overlapped with the data-generating parameters in all but one parameter, the regression coefficient for stand age ( $\beta_3$ ), indicating a generally good fit (Figure 5; DiRenzo et al. 2023). The empirical model indicated a stronger effect of stand age than was detected in the validation model, potentially due to small sample sizes, but the parameter estimate of the empirical model was only slightly outside of the 95% credible interval.

## DISCUSSION

Our results suggest that the biotic and abiotic conditions in Adirondack Park are more challenging for breeding fishers than the adjacent Tug Hill Plateau, which may explain the perceived decrease in fisher density within Adirondack Park in recent years (New York State Department of Environmental Conservation 2015). While density dependence can lead to decreased recruitment with increased densities (Ferrer and Donazar 1996), spacing of the adult females is also dependent on resources (Fretwell and Lucas 1970, Fretwell 1972). Thus, high densities might be associated with greater resource abundance, and therefore a higher threshold before the effects of density dependence depress kit survival and recruitment. While we observed greater time away from the den when females were foraging further, we did not detect effects of forest stand age, which we expected to be indicative of prey availability and abundance. However, kit survival rates within Adirondack Park were generally more variable than observed in the Tug Hill Plateau. This could be an artefact of differences in the number of counts per litter, as the standard deviation of counts in the Tug Hill Plateau was approximately half of the standard deviation of Adirondack counts. Yet, because fishers tend towards slow life history traits, such as late sexual maturity and long interbirth intervals (Ferguson and Larivière 2002, 2005), juvenile survival is expected to vary in response to suboptimal conditions (Gaillard et al. 1998), which we suggest is likely the case across a gradient of forest stand age, as well as other landscape conditions, in northern New York.

Tree cavities, in live or dead trees, are thought to protect kits from predators and the elements (Raley et al. 2012, Matthews et al. 2019), and therefore female fishers are restricted to habitat that contains a suitable number of these structures (Weir et al. 2012). Several studies have shown the importance of plentiful large diameter trees for fishers to use as den sites (Berg et al.

2020). A limited supply of suitable den structures is likely to be a source of density dependence (Weir et al. 2012), though old forests generally have a higher frequency of such structures (Bell et al. 2021). We might assume that the Tug Hill Plateau, with generally younger average stand age (Pan et al. 2011) might be limiting in this regard, but our results showing smaller home range sizes and shorter travel distances, in addition to consistently higher numbers of young fishers harvested from the Tug Hill (Chapter 4) indicate otherwise. In western North America, it has been suggested that the areas suitable for reproduction may not offer the best prey availability (Raley et al. 2012), and prey availability rather than suitable denning opportunities may be more limiting to fisher within NY State. Indeed, fishers have expanded across New York to habitats that were previously considered unsuitable (e.g., suburban habitats; LaPoint et al. 2013, Scharf et al. 2016). Therefore, we suggest that older forests, despite offering plentiful den cavities, likely are lower quality in terms of prey availability.

Prey abundance, accessibility, and diversity on the landscape is linked to space use and reproduction in several predatory species (Bengsen et al. 2016, Kirby et al. 2018, Coon et al. 2020). Mesocarnivores such as red (*Vulpes vulpes*) and arctic foxes (*V. lagopus*) select den locations based on prey availability, abundance, and distribution (Eide et al. 2004, Szor et al. 2008, Gallant et al. 2014), while raptor productivity varies with prey density (Salafsky et al. 2005). We suspect that the gradient of forest stand age across northern New York represents variation in key prey for fishers, especially considering the larger average home range sizes of Adirondack females (Figure 3) in addition to lower and more variable kit survival. For example, snowshoe hare (*Lepus americanus*), an important prey item for fishers (Powell 1993), often use forests <40 years old (Kawaguchi and Desrochers 2018), and the aging Adirondack forests have exhibited a long-term decline in hare abundance (NYS DEC, unpublished data). However,

fishers are generalist predators (McNeil et al. 2017, Happe et al. 2021, Smith et al. 2022), and we would expect that the ability to switch to prey items may mediate the effects of low densities of specific prey items (Randa et al. 2009), such as snowshoe hares. Yet, a lack of suitable alternative prey sources can lead to depressed reproductive capacity in a population (Suryan et al. 2000) and an overall population decline (Kirby et al. 2018). Additionally, when prey density or accessibility is low, spending time outside of the den to forage puts females at greater risk of encountering other predators because higher activity levels tend to increase exposure relative to fishers that can go longer between meals. In California, Wengert et al. (2014) found that bobcats killed significantly more female than male fishers, and that nearly three quarters of the fishers killed were between March and July, when kits were still dependent on the mother (Powell 1993). Thus, prey availability may impact recruitment directly through kit survival as well as indirectly via risks to the mother.

We also interpret the positive association between WUI and kit survival as related to prey availability. We observed several den trees located within a kilometer of buildings (Figure 6). Mountain lion body condition has been positively linked to the types of marginal development found in WUI, potentially due to increased abundance of raccoon (*Procyon lotor*) and gray squirrel (*Sciurus carolinensis*) prey (Coon et al. 2019), both of which are consumed by fishers (Powell et al. 1997). Edge habitats, such as those created by development, often have high densities of small mammals (Osbourne et al. 2005), and thus offer ideal foraging areas for predators (Šálek et al. 2010). Therefore, we suspect that fishers in areas with WUI have access to greater diversity or abundance of prey, despite the increased risk of anticoagulant rodenticide poisoning (Chapter 3). Notably, the female that lost her litter and the female that died during the denning period were both on the low end of the range of WUI ranges.

We noted an alternative-year pattern in number of denning female fishers in our focal areas, especially within the Adirondack Park, though sample sizes were small (Table 2), which may be indicative of a response to mast cycles. American beech (*Fagus grandifolia*) is the primary hard mast-producing species in the Adirondack region (McNulty and Masters 2005), and State University of New York College of Environmental Science and Forestry researchers at the Huntington Wildlife Forest near Newcomb, NY have recorded data on beechnut production since 1988. Their records indicated mast seedings in August–November 2019 and 2021, which immediately preceded denning periods where 75–77% of collared breeding age female fishers were observed with kits. In contrast, following the mast failures recorded in 2020, we observed only 3 of 18 breeding-age females with kits (17%; Table 2). Fisher populations have been shown to respond to mast crops both in harvest vulnerability (Jensen et al. 2012, Chapter 4) and numerical increases related to increases in small mammal abundance (Jensen et al. 2012, Greenhorn et al. 2021). However, small mammal populations do not increase until the spring or summer after mast crops, and therefore we speculate that this pattern could be a result of increased winter food availability of the beechnuts themselves, as over-winter prey availability can influence breeding propensity (Orlando et al. 2023), if not juvenile survival. Further, we monitored three female fishers over two breeding seasons each, and all were only observed denning in one of the years they were observed, providing anecdotal evidence for alternate-year breeding schedules.

Contrary to our expectations, we did not detect effects of cold spring temperatures on kit survival. It is possible that our sample size of 19 breeding females was too small, or there was insufficient variability among individuals or years, to detect effects. Alternatively, mortality due to extreme cold could occur prior to the first relocation; our probabilistic estimate of initial litter

size may not capture this effect. Additionally, minimum temperature (via residuals) trended towards the expected relationship—we hypothesized that extreme cold temperatures would increase the amount of time spent in the den—the parameter estimates were very small (Figure 1). Stand age had a moderate relationship with bout duration, but not as strong as we had expected, but also in the opposite direction. The effects of number of kits on the proportion of the day spent in the den was opposite of what we expected; we hypothesized that having more kits would require females to spend more time out foraging and less time in the den. Yet, we do not have measurements on the relative difference in energy intake requirements for differences in just one or two kits, and it may be only the largest litters that require additional time away to forage. We did not detect an effect of maternal age on kit survival. Our set of female fishers likely included both first-time mothers (2-year-olds), as well as females that may have had previous litters. This lack of effect was surprising given demonstrated differences in reproductive costs and resource acquisition related to maternal age (Rauset et al. 2015), and may have been a result of insufficient power in our model to identify differences. However, Matthews et al. (2019) also failed to detect an effect of maternal age on litter survival (i.e., at least one kit surviving) across 31 litters.

Our kit survival models were based on several assumptions. The unmarked young survival model (Lukacs et al. 2004), and by extension our model for kit survival, assumed that offspring within a brood or litter are interchangeable. Though there is some evidence for higher growth rates in males (Matthews et al. 2019 and references therein), we do not have a strong reason to assume violation of this assumption as several studies have shown mean body mass between male and female kits to be similar for approximately 90 days (Powell 1993, Frost and Krohn 2005). The kit survival model further assumed that daily survival probabilities were

constant throughout the denning period. Studies of captive fishers indicate the majority of kit deaths occurs early in the denning period, before our monitoring of kit counts began, usually as a result of exposure and maternal neglect (Frost and Krohn 1994), and similar patterns have been observed in wild fishers (Matthews et al. 2019). Because we did not attempt cavity checks and instead depended on photo captures for kit counts, it is difficult to capture the differences in survival rates in the early days, even with probabilistic estimates of initial litter size. Therefore, we interpret our estimated kit survival rates as an average, and potentially slightly higher than true kit survival. Relatedly, our probabilistic estimates of initial litter size are potentially biased low, though the model estimate of 3.40 kits per female is higher than litter sizes observed by Frost and Krohn (1994).

While we interpret our results cautiously, we have demonstrated the applicability of young survival models adapted to fisher kit survival which may be informative for studies on other denning species. For example, similar monitoring methods are used for marten (e.g., *Martes americana* and *M. caurina*; Delheimer et al. 2021) and fisher populations in western North America, several of which are of conservation concern (Fogarty et al. 2022, Lofroth et al. 2023). With larger sample sizes, we expect that modeling fisher kit survival with extensions of the unmarked young survival model (Lukacs et al. 2004) will be able to answer questions on much finer scales than estimating kit and litter survival based purely on proportion of litters being weaned (Sweitzer et al. 2015). Additionally, we provide one of the first in-depth investigations into fisher reproductive ecology in the northeastern United States in nearly two decades, though challenges remain in quantifying juvenile survival between weaning and independence. The use of regular den sites declines after kits are weaned (Aubry and Raley 2006), and along with it, researchers' ability to relocate females and obtain counts.

The challenges for fisher related to prey acquisition and reproduction are likely to persist with future global change. Climate change is expected to result in increased temperatures throughout the fisher's range (Lawler et al. 2012), though warming in the Adirondack region 1990–2020 occurred mostly July–September (Stager et al. 2022), therefore we do not anticipate direct effects of climate change on late winter/spring kit survival. Yet, the effects of climate change have already been observed on key fisher prey species, snowshoe hares (Diefenbach et al. 2016), and warming may decrease the abundance of deer carrion (Weiskopf et al. 2019). The introduced beech bark disease may also decrease food availability prior to and during the kit rearing period by reducing mast production and subsequent small mammal populations (Rosemier and Storer 2010), though oaks (*Quercus spp.*), producers of mast crops, are predicted to expand their ranges northward into the Adirondack Park as a result of climate change (Iverson et al. 2008, Matthews et al. 2011) with acorn production likely to increase as well (Shibata et al. 2020, Touzot et al. 2020). Further, despite the 'Forever Wild' clause of the New York State constitution controlling development and forest management, the Adirondack Park contains several towns (Porter et al. 2009) and sees as many as 12 million visitors each year (Schneller et al. 2021). Extensive ranging for prey in these developed areas may also increase direct (e.g., vehicle strikes; Paragi et al. 1994) or indirect mortality risks (e.g., rodenticide poisoning; Chapter 3, Thompson et al. 2014) to breeding females. Two of our collared females in the Adirondack Park, determined to have two and four kits in utero, was found near roads. One was found dead due to trauma from a vehicle strike, and the other was humanely dispatched by a conservation officer. The euthanized female tested positive for all of the three most-detected anticoagulant rodenticide compounds in New York (bromadiolone, brodifacoum, and diphacinone; Chapter 3) at high—likely lethal—concentrations.



While fisher populations were restricted to the Adirondack Park by the early 20<sup>th</sup> century, after extirpation due to land use conversion and intensive trapping, they have successfully rebounded throughout much of their former range in the northeastern United States (Lewis et al. 2012, LaPoint et al. 2015). Yet, the Adirondack region of northern New York has historically been a low-productivity system (Porter 2009), and revised assessments of fisher habitat selection and requirements indicate that fishers may not be the mature-forest specialists they were once thought to be (Buskirk and Powell 1994, Raley et al. 2012). Thus, fishers in the Adirondack Park are already at a disadvantage, and as a result may require different management strategies (e.g., harvest bag limits, establishment of refugia from harvest) than fishers in more productive regions of New York in order to maintain stable population density.

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## TABLES

**Table 1:** Summary of estimated parturition dates, camera set dates, kit counts for each female fisher in the Tug Hill and Adirondack regions of northern New York State. Female age (in years) estimated from birthday of 1 April.

Year / Fisher	Study Area	Maternal Age (years)	Estimated parturition date	First cameras set	Dens Identified	# times kits counted <sup>c</sup>	Maximum count	End count
<i>2020</i>								
19F501	ADK	3	28-Mar	23-Mar	3	1	2	2
19F503	ADK	2	14-Mar	20-Mar	4	2	3	3
20F501	ADK	5	21-Mar <sup>a</sup>	23-Mar	1	1	1	NA
20F610	THP	2	26-Mar	26-Mar	5	3	2	2
20F614	THP	4	19-Mar	24-Mar	4	2	3	2
20F615	THP	5	25-Mar	24-Mar	3	3	2	2
<i>2021</i>								
20F612	THP	5	2-Apr	5-Apr	3	2	3	3
20F617	THP	3	25-Mar	5-Apr	4	3	3	3
20F621	THP	3	28-Mar	1-Apr	4	3	1	1
<i>2022</i>								
19F504	ADK	4	26-Mar	28-Mar	5	3	1	1
20F504	ADK	3	9-Apr	12-Apr	4	5	2	2
21F507	ADK	3	28-Mar <sup>a</sup>	7-Apr	1	1	3	0
21F508	ADK	2	28-Mar <sup>a</sup>	28-Mar	4	3	3	3
22F502	ADK	2	28-Mar <sup>a</sup>	30-Mar	5	4	2	1
22F505	ADK	2	26-Mar	31-Mar	3	2	2	1
19F603	THP	4	21-Mar <sup>a</sup>	1-Apr	4	3	4	4
20F607	THP	3	27-Mar	11-Apr	5	2	3	3
21F606	THP	3	21-Mar <sup>a</sup>	25-Apr	1	1	2	NA
21F611	THP	4	15-Mar	6-May <sup>b</sup>	3	2	4	4

<sup>a</sup>Average of study area/year filled in for females with VHF collars

<sup>b</sup>Den on private land, permission not granted for entry until much later in the denning period

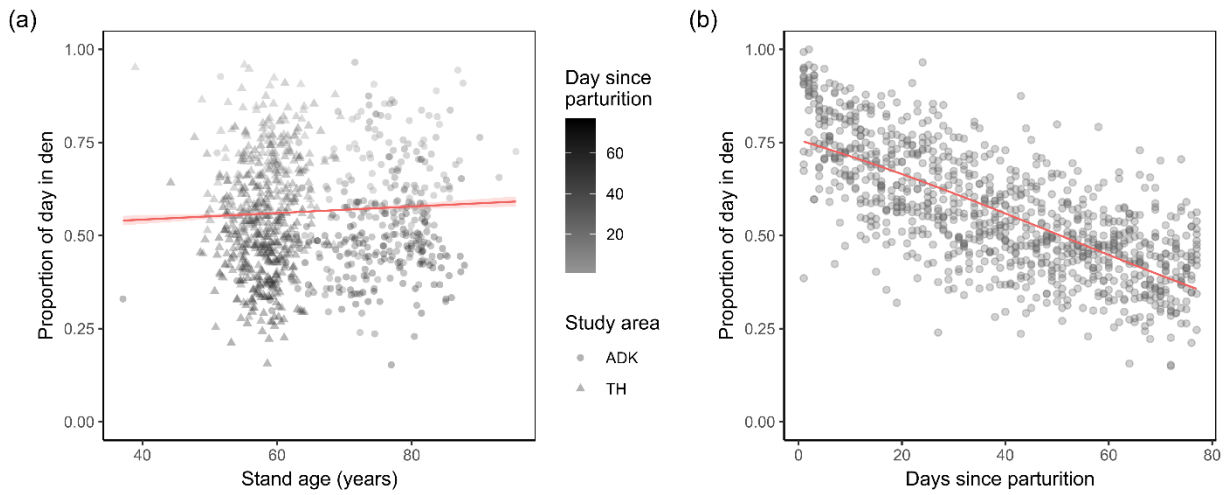
<sup>c</sup>Excludes days when kits were crawling under their own power

**Table 2:** Number of female fishers  $\geq 2$  years old as of April of each year that were monitored and observed with kits in the Tug Hill Plateau (THP) and Adirondack (ADK) focal areas of northern New York.

Year	Females monitored			Observed with kits			Proportion with kits		
	THP	ADK	Total	THP	ADK	Total	THP	ADK	Total
2019	1	2	3	0	0	0	0	0	0
2020	5 <sup>a</sup>	3	8	3 <sup>a</sup>	3	6	0.60	1.0	0.75
2021	10	8	18	3	0	3	0.30	0	0.17
2022	5	8	13	4	6	10	0.80	0.75	0.77

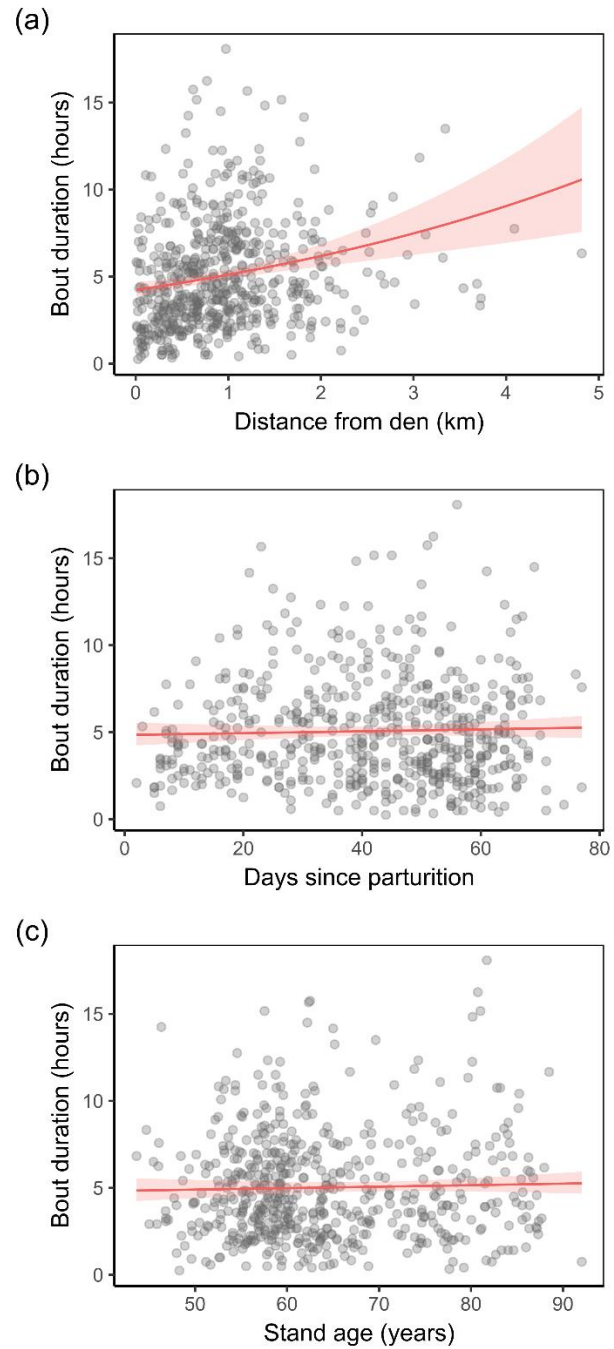
<sup>a</sup>One additional female was observed later on camera with kits, but her collar malfunctioned shortly after capture on 2020-03-04

## FIGURES

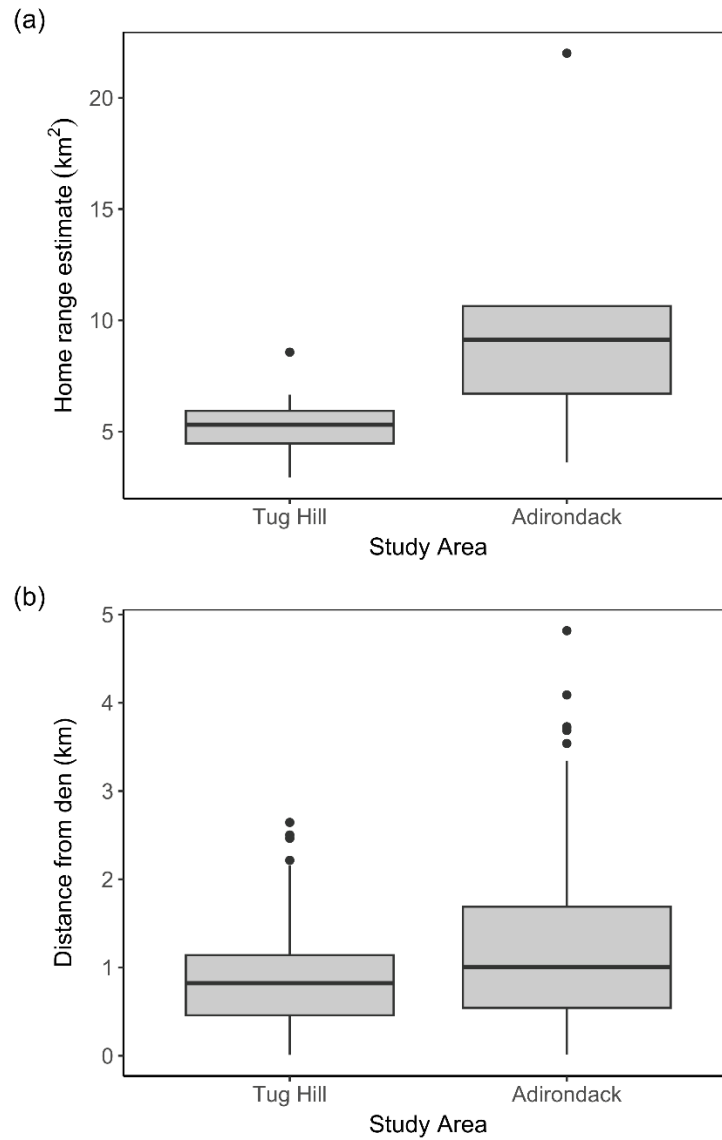


**Figure 1:** Predicted (red line) and observed (gray points) proportion of time female fishers across northern New York spent in the den as a function of forest stand age (in years) and days since parturition.

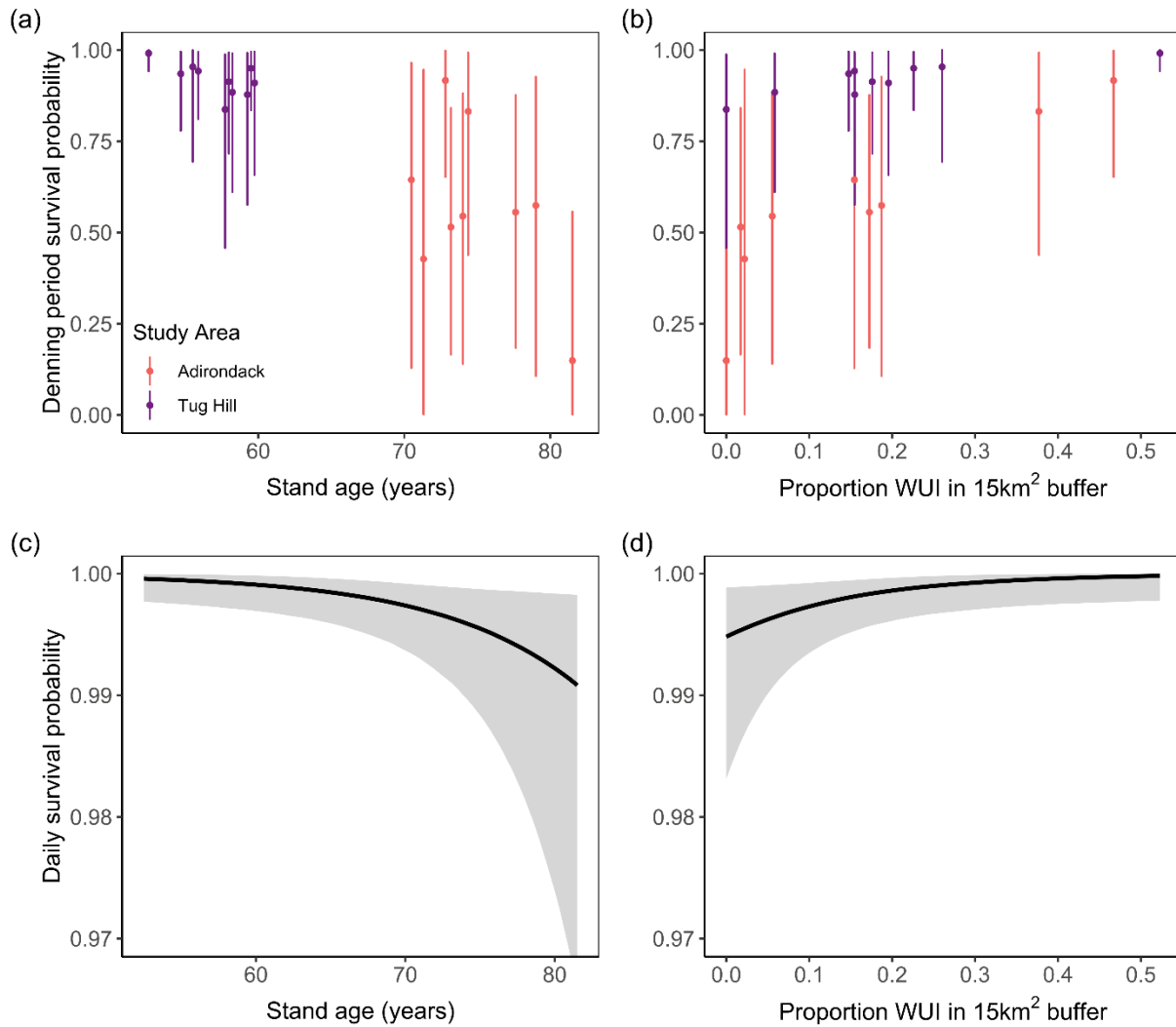




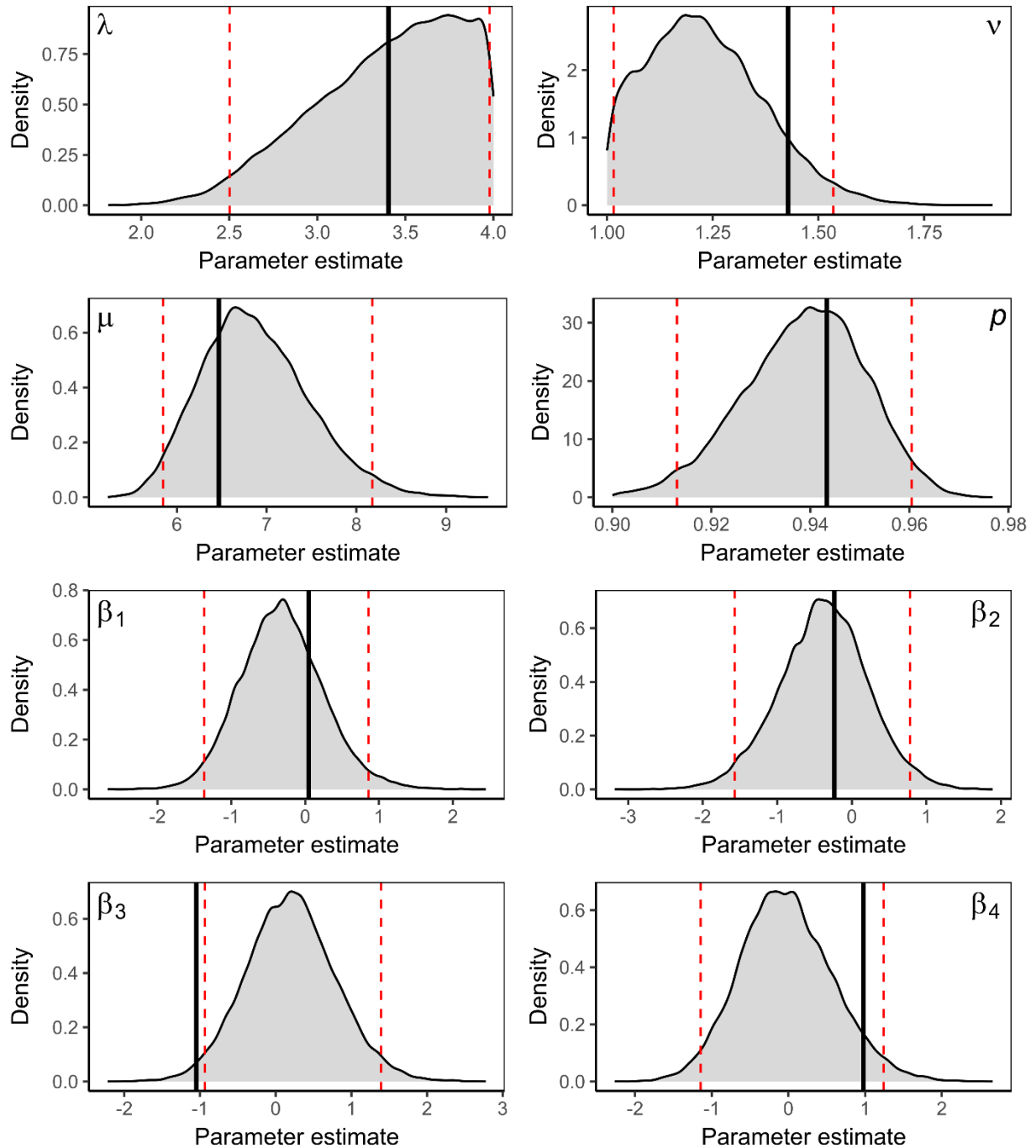
**Figure 2:** Predicted foraging bout duration (in hours) of denning female fishers according to average foraging distance from the den (red line and shading = mean and 95% Bayesian credible interval). Observed bout durations and distances shown during the 11-week denning period.



**Figure 3:** Comparison of space use by breeding female fishers, specifically (a) distribution of home range estimates ( $\text{km}^2$ ) by study region (Tug Hill Plateau in the west and the Adirondack Park in the east) estimated via 95% autocorrelated kernel density estimation, and (b) distance between GPS locations and reproductive dens during foraging bouts.

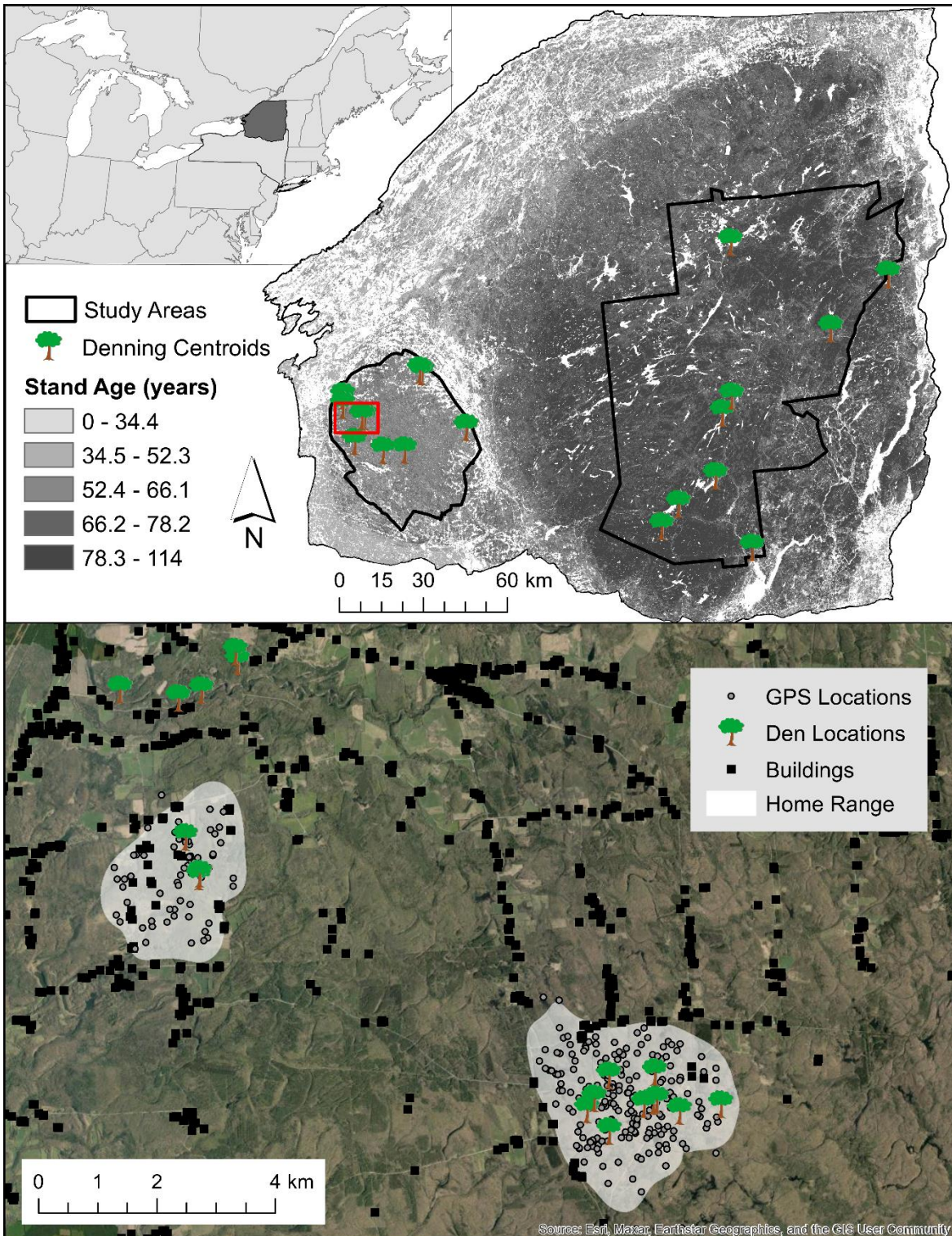


**Figure 4:** Relationship between forest stand age and fisher kit survival in northern New York, 2020–2022. Upper panels show the estimated 11-week denning period survival probability for kits reared by each female fisher plotted against (a) stand age (within 15 km<sup>2</sup> buffer) and (b) proportion of WUI. Lower panels show the predicted effects of (c) stand age and (d) proportion of WUI on daily fisher kit survival.



**Figure 5:** Posterior densities from basic validation model of kit survival model. We used the parameter estimates from the model (vertical black lines) to simulate a new data set, for which the posterior densities are shown, with dashed red lines delineating the 95% Bayesian credible interval (BCI) of the posterior distribution. Ideally, the 95% BCI of the simulated dataset should

contain the mean parameter estimate used to generate the new data set. Parameters shown are mean litter size ( $\lambda$ ), dispersion parameter for litter size ( $\nu$ ), intercept in linear predictor for daily survival rate ( $\mu$ ), probability of detection for kits ( $p$ ), and regression coefficients for maternal age ( $\beta_1$ ), number of days below freezing ( $\beta_2$ ), stand age ( $\beta_3$ ), and wildland-urban interface ( $\beta_4$ ).



**Figure 6:** Distribution of den locations across northern New York against the backdrop of forest stand age (top), and subset of 95% AKDE home ranges, GPS points, and den locations in relation to the distribution of dwellings and other structures. Denning centroids refers to the

center point of all identified den trees for each female. Red rectangle in top panel is the zoomed-in area in the bottom panel. The den locations in the top left corner of the bottom panel were used by a female fisher with a VHF-only collar, so we were unable to calculate a home range.

## Appendix 5-1. Distribution of bout duration.

**Table A1.** Comparison of bout duration (in hours) fit to different distributions via the *fitdistrplus* package.

<b>Distribution</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Gamma	12419.6	0
Weibull	12423.5	3.9
Exponential	12544.0	124.3
Log-normal	12628.3	208.7



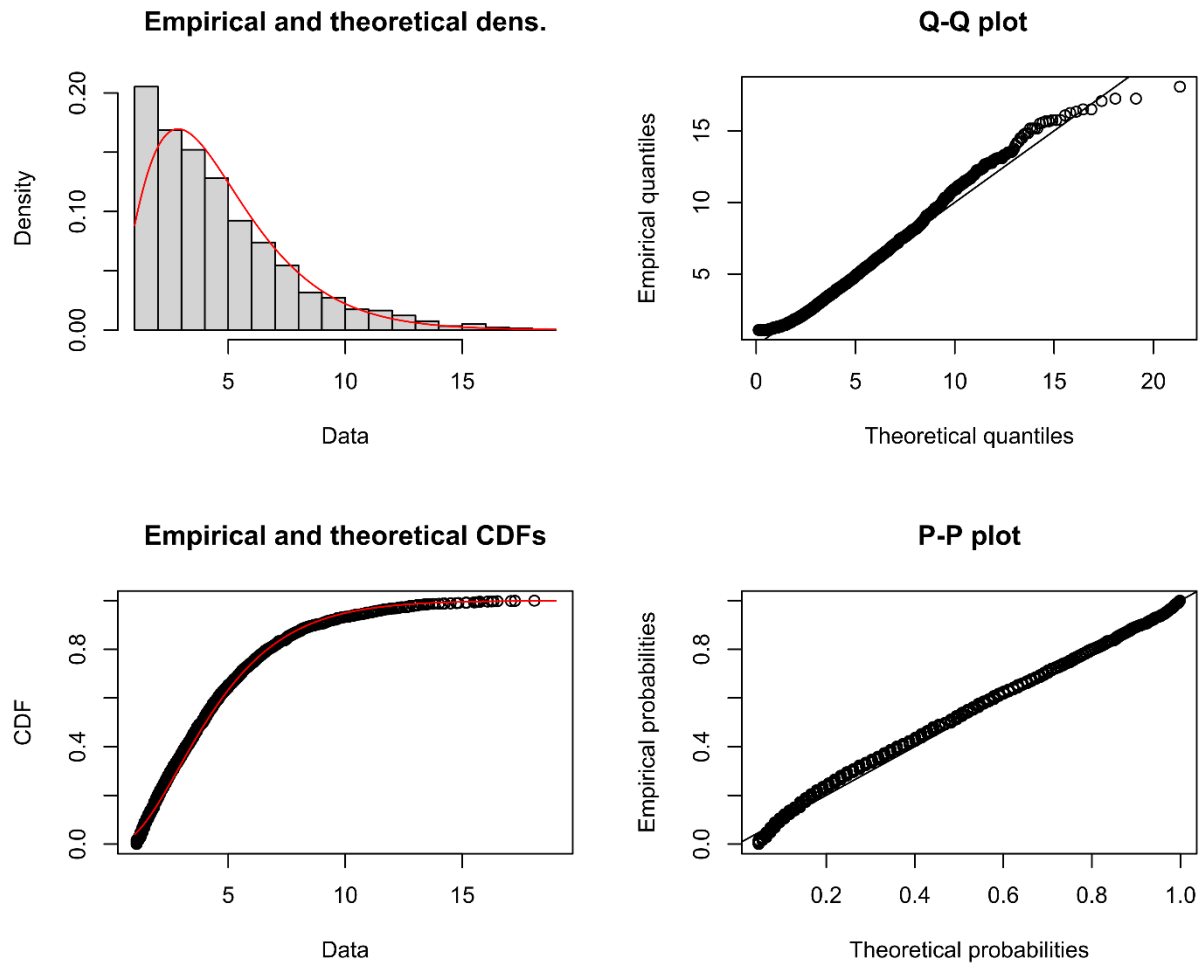


Figure A1. Diagnostic plots for bout duration modeled as a gamma regression.

Table A2. Distances (m) used as initial values for bout duration model for each individual.

<b>Individual</b>	<b>Study area</b>	<b>Average Distance (m)</b>	<b>Number of bouts</b>
19F501	Adirondack	639.8	53
19F503	Adirondack	1450.5	51
19F504	Adirondack	1186.6	20
20F504	Adirondack	1912.2	36
20F607	Tug Hill	537.4	34
20F610	Tug Hill	705.9	57
20F612	Tug Hill	836.0	56
20F614	Tug Hill	1066.1	41
20F615	Tug Hill	852.7	88
20F617	Tug Hill	818.4	47
20F621	Tug Hill	1370.7	37
21F611	Tug Hill	452.7	25
22F505	Adirondack	889.8	40

## Appendix 5-2. Kit survival model

Table A3. Correlation matrix for covariates included in kit survival model. Spatial variables (wildland-urban interface, stand age) based on 15 km<sup>2</sup> circular buffer around center of denning area.

	<b>Maternal age</b>	<b>Wildland-urban interface</b>	<b>Stand age</b>
<b>Wildland-urban interface</b>	$r = -0.04, P = 0.88$ (95% CI: -0.48, 0.42)		
<b>Stand age</b>	$r = -0.34, P = 0.16$ (95% CI: -0.67, 0.14)	$r = -0.19, P = 0.44$ (95% CI: -0.59, 0.29)	
<b>Cumulative freeze days</b>	$r = -0.14, P = 0.55$ (95% CI: -0.56, 0.33)	$r = -0.08, P = 0.75$ (95% CI: -0.51, 0.39)	$r = 0.38, P = 0.11$ (95% CI: -0.09, 0.71)

## CHAPTER 6: CONCLUSIONS

In this dissertation, I investigated survival and productivity (via kit production and survival) of fishers (*Pekania pennanti*) across New York, as well as potential individual, temporal, and spatial characteristics that contribute to differences in them. This research was motivated by an observed apparent decline of fisher catch-per-unit-effort (CPUE) over 10-15 years in the Adirondack region of northern New York (New York State Department of Environmental Conservation 2015) and funded by the NY State Department of Environmental Conservation who contributed to the work and will readily use the results in management planning. Together we sought to investigate potential demographic sources of this apparent decline. My second chapter established detection probabilities for using camera traps to assess kit survival (via counts) and maternal den attendance and will be informative for future researchers using similar methods. My third chapter investigated anticoagulant rodenticide exposure in relation to landscape characteristics and beech mast cycles. I found that the number of expected compounds that fishers were exposed to increased with wildland-urban intermix, and increased following beech (*Fagus grandifolia*) mast events. In my fourth chapter, I estimated annual survival rates of fishers across gradients of landscape characteristics across northern New York, identified harvest as the primary driver of mortality in the Tug Hill focal area, and provide evidence that even the low level of harvest observed for Adirondack fisher may tend towards additive versus compensatory mortality. My fifth chapter investigated maternal space use and den attendance patterns as well as fisher kit survival and revealed a pattern of lower kit survival and increased home range sizes of fishers in the Adirondack Park. Overall, this dissertation presents evidence for differences in population dynamics between the Adirondack Park and other

nearby areas of northern New York, in which reproduction and survival are limited in the Adirondack Park, likely a result of prey limitations in the over-mature “Forever Wild” forests.

The role of prey in regulating predator space use (Nilsen et al. 2005, Ferguson et al. 2009, Mitchell and Powell 2012) and population dynamics has been the subject of extensive investigation (King et al. 2003, Elmhagen et al. 2010, O’Neil et al. 2017). The Adirondack region was historically low productivity with limited natural disturbances (Porter 2009), but remained the last foothold in New York for fishers to prevent complete extirpation in the late 19<sup>th</sup> and early 20<sup>th</sup> centuries (Krohn 2012). Given that the ‘Forever Wild’ clause in the New York State constitution limits the extent of development and forest management (Porter et al. 2009), much of the park consists of old-growth or second-growth forest that is now mature forest that has not been disturbed since the early 20<sup>th</sup> century (Ziegler 2000). I used forest stand age, which generally increased from west to east, as a proxy for prey availability for fishers in northern New York. While stand age did not explain variation in adult survival (Chapter 4), it was important for kit survival (Chapter 5).

This dissertation underscores the importance of beech mast cycles in fisher population dynamics. Fishers consume beechnuts directly, as well as the small mammals that increase after the production of mast crops (Jensen et al. 2012, Greenhorn et al. 2021). I found clear relationships between survival and mast year, with decreased risk of mortality due to harvest in mast years (Chapter 4), increased breeding propensity following masting events (Chapter 5), and increased exposure anticoagulant following masting events (Chapter 3). The latter observation presents a paradox, because large mast crops may provide significant resources for fishers, may also present a risk of poisoning. The dosage of anticoagulant rodenticides required for an individual to present clinical symptoms is unknown, and it likely varies between male and

female fishes, but even sublethal effects can impact population growth rates (Martínez-Padilla et al. 2017, Roos et al. 2021). Thus, if rodenticide exposure continues to increase, the link to beech mast could result in a phenomenon similar to an ecological trap, especially when alternative food sources are scarce (Geduhn et al. 2016). However, one may anticipate higher exposure years and use that information to target educational campaigns and ensure wide availability of snap traps as relative low-cost mitigation effort.

Presently, fishers in the northeastern United States may be sheltered from some of the more putative damaging effects of climate change. West coast fisher populations experience loss of suitable habitat and denning structures as a result of increasingly intense wildfires (Lawler et al. 2012), in addition to considerations for much higher levels of timber harvest (Zielinski and Schlexer 2019, Green et al. 2022). Yet, the Northeast contains high human population densities in close proximity to forests (Sonti et al. 2023). Human activities will continuously be a potential challenge with a greater impact than climate change, but may benefit fishers by providing or concentrating additional food sources (e.g., raccoons [*Procyon lotor*] or eastern gray squirrels [*Sciurus carolinensis*]; Powell et al. 1997). My results indicated that risk of mortality decreased in areas with wildland-urban interface (WUI; Chapter 4), which was unexpected given the relationship between WUI and anticoagulant rodenticide exposure (Chapter 3). Even my examination of prothrombin time, a metric for blood clotting expected to increase with rodenticide exposure (Hindmarch et al. 2019), did not explain variation in survival. Our sample sizes were too small to statistically examine the link between prothrombin time and productivity, but a pattern was not evident from visual inspection of available data. I suspect that despite the risk of rodenticide exposure, heterogeneity from disturbance in the WUI provide greater prey availability or accessibility for fishers. Additionally, because WUI includes human dwellings, fur

trappers may be hesitant to trap too close to these areas (Triezenberg and Knuth 2018), thus creating de facto harvest refugia. Yet, WUI forests may have less structural complexity (Sonti et al. 2023), which is an important aspect of fisher habitat (Raley et al. 2012), and as demonstrated previously higher exposure risks for rodenticides.

#### **FUTURE RESEARCH RECOMMENDATIONS**

While this dissertation provides insight into spatial variation in fisher demographic rates, additional research may complement what has been done here to further assist in fisher management across the state. First, Chapter 5 indicated differences in home range size for fishers in the Tug Hill Plateau and within the Adirondack Park. Energetic requirements for reproductive females are nearly 3 times that of non-reproductive periods (Powell and Leonard 1983), underscoring the importance of prey availability for breeding females. Additionally, the proportion of females giving birth in a given year is likely dependent on prey availability throughout the winter (Krohn et al. 1995, Frost and Krohn 1997). Therefore, low prey abundance may impact recruitment via multiple routes, including breeding propensity and kit survival. Future research might investigate variation in an individual's home range during the denning period compared to when females do not have dependent kits, as well as resource selection of breeding compared to non-breeding females. Similarly, in-depth diet analyses via stable isotopes would likely provide information on prey diversity, which could also be related to overall condition of fishers, and subsequent population growth rates (Kirby et al. 2018).

Finally, while I identified areas of lower productivity, greater space use, and higher natural mortality, it was beyond the scope of my dissertation to examine dispersal and movement rates of fishers in northern New York. Within a species, these demographic parameters can vary

spatially, sometimes to the extent that certain habitats have higher mortality than productivity and cannot persist without an influx of new individuals (Pulliam 1988). Immigration and emigration are important processes in maintaining metapopulations (Gyllenberg and Hanski 1997, Hanski 1998), especially so-called ‘sink’ populations (Pulliam 1988, Pulliam and Danielson 1991). I observed at least one animal dispersing >85 km away from the center of the Adirondack Park (ending up near the High Peaks Wilderness), and another that may have dispersed over 55 km to the south of the park. Comparison of dispersal distances between the Adirondack Park and more productive regions (e.g., Tug Hill Plateau), together with estimates of survival and productivity, would be a better indication of the extent of source and sink habitats in northern New York.

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## CURRICULUM VITAE

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#### EDUCATION

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- 2023 **Doctor of Philosophy in Ecology**  
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- 2019 **Master of Science in Natural Resources** with emphasis in Fish & Wildlife Science; Graduate minor in Statistics  
University of Missouri, *Columbia, MO*
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#### RESEARCH

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- 2019-present **Influence of landscape gradients on fisher (*Pekania pennanti*) survival and productivity in New York State**  
PhD Dissertation, SUNY College of Environmental Science and Forestry  
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- 2017-2019 **Decision-making and Demography of Greater White-fronted Geese**  
MS Thesis, University of Missouri  
Supervisor: Mitch D. Weegman, PhD

#### PEER-REVIEWED PUBLICATIONS

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**Cunningham SA**, Schafer TLJ, Wikle CK, VonBank JA, Ballard BM, Cao L, Bearhop S, Fox AD, Hilton GM, Walsh AJ, Griffin LR, and MD Weegman. 2023. Time-varying effects of local weather on behavior and probability of breeding deferral in two Arctic-nesting goose populations. *Oecologia* 201: 369-383. DOI: [10.1007/s00442-022-05300-x](https://doi.org/10.1007/s00442-022-05300-x)

VonBank JA, Schafer TLJ, **Cunningham SA**, Weegman MD, Link PT, Kraai KJ, Wikle CK, Collins DP, Cao L, and BM Ballard. 2023. Joint use of location and acceleration data reveals drivers of transitions among habitats in wintering birds. *Scientific Reports* 13: 2132. DOI: [10.1038/s41598-023-28937-x](https://doi.org/10.1038/s41598-023-28937-x)

Schindler AS, **Cunningham SA**, Schafer TLJ, Sinnott EA, Clements SJ, DiDonato FM, Mosloff AR, Walters CM, Shipley AA, Weegman MD, and Q Zhao. 2022. Joint analysis of structured and semi-structured community science data improves precision of relative abundance but not trends in birds. *Scientific Reports* 12: 20289. DOI: [10.1038/s41598-022-23603-0](https://doi.org/10.1038/s41598-022-23603-0)

**Cunningham SA**, Pyszczyński T, Watson T, Bakerian R, Jensen PG, and JL Frair. 2022. Detecting denning behavior with camera traps: An example with fishers. *Wildlife Society Bulletin* 46(2): e1371. DOI: [10.1002/wsb.1371](https://doi.org/10.1002/wsb.1371)

**Cunningham SA**, Zhao Q, and MD Weegman. 2021. Increased rice flooding during winter explains the recent increase in the Pacific Flyway White-fronted Goose *Anser albifrons frontalis* population in North America. *Ibis* 163(1): 231-246. DOI: [10.1111/ibi.12851](https://doi.org/10.1111/ibi.12851)

VonBank JA, Weegman MD, Link PT, **Cunningham SA**, Kraai KJ, Collins DP, and BM Ballard. 2021. Winter fidelity, movements, and energy expenditure of midcontinent greater white-fronted geese. *Movement Ecology* 9: 2. DOI: [10.1186/s40462-020-00236-4](https://doi.org/10.1186/s40462-020-00236-4)

Stabach JA, **Cunningham SA**, Connette G, Mota JL, Reed D, Byron M, Songer M, Wacher T, Mertes K, Brown JL, Comizzoli P, Newby J, Monfort S, and P Leimgruber. 2020. Short-term effects of GPS collars on the activity, behavior, and adrenal response of scimitar-horned oryx (*Oryx dammah*). *PLoS ONE* 15(2): e0221843. DOI: [10.1371/journal.pone.0221843](https://doi.org/10.1371/journal.pone.0221843)

## CONFERENCE POSTERS AND PRESENTATIONS

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### *Contributed Talks*

- 2023           Cunningham SA, JL Frair, Buckles EL, Jensen PG, and KL Schuler. Rodenticide exposure and potential productivity in fishers across New York. 78<sup>th</sup> Annual Northeast Association of Fish and Wildlife Agencies Conference, Hershey, PA.
- 2023           Cunningham SA, Pyszczyński T, Watson TM, Bakerian R, Jensen PG, and JL Frair. Utility of camera traps for assessing productivity in a forest carnivore. Northeast Natural History Conference, Burlington, VT.
- 2022           Cunningham SA, Watson TM, Pyszczyński T, Jensen PG, and JL Frair. Investigating spatial variability in fisher survival rates in northern New York. The Wildlife Society Annual Conference, Spokane, WA.
- 2021           Cunningham SA, Jensen PG, and JL Frair. Camera deployment for optimal detection of critical life events in a forest community. 76<sup>th</sup> Annual Northeast Fish & Wildlife Conference, Virtual.
- 2019           Cunningham SA, Schafer TLJ, Wikle CK, Ballard BM, VonBank JA, Bearhop S, Hilton, GM, Walsh AJ, Griffin L, Fox AD, and MD Weegman. A new horizon: the utility of acceleration data to quantify the fitness implications of behaviors in migratory birds. *Society of Canadian Ornithologists, Quebec City, QC, Canada*.
- 2019           Cunningham SA, Schafer TLJ, Wikle CK, Ballard BM, VonBank JA, Bearhop S, Hilton GM, Walsh AJ, Griffin L, Fox AD, and MD Weegman. Quantifying behavioral and environmental impacts on reproduction attempts in long-distance migratory geese of contrasting life history. *Ecological Society of America Annual Meeting, Louisville, KY*.
- 2019           Cunningham SA, Schafer TLJ, Wikle CK, Ballard BM, VonBank JA, Bearhop S, Hilton GM, Walsh AJ, Griffin L, Fox AD, and MD Weegman. Quantifying trade-

offs in migration and reproduction in long-distance migratory birds of contrasting life history. *American Ornithological Society Annual Meeting, Anchorage, AK.*

- 2018 Cunningham, SA, Weegman MD, and BM Ballard. The green wave and migration in Arctic-nesting geese: is mismatch detrimental? *North American Arctic Goose Conference, Lincoln, NE.*
- 2016 Cunningham SA, Birt M, Eyres A, Haefele H, Packard JM, and JA Stabach. Behavior of scimitar-horned oryx wearing GPS collars. *Smithsonian Conservation Biology Institute Student Symposium, Front Royal, VA.*

#### *Contributed Posters*

- 2021 Cunningham SA, Pyszczyński T, Watson TM, Bakerian R, Jensen PG, and JL Frair. Camera deployment for optimal detection of critical life events in fisher. *The Wildlife Society Annual Meeting, Virtual.*
- 2019 Cunningham SA, Zhao Q, and MD Weegman. Understanding drivers of population growth in white-fronted geese. *Missouri Natural Resources Conference, Osage Beach, MO.*

#### **GRANTS AND FELLOWSHIPS**

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- 2023 **Moore Family Fund for Conservation Scholarship**, SUNY College of Environmental Science and Forestry – \$1500
- 2022 **Wilford A. Dence Fellowship**, SUNY College of Environmental Science and Forestry – \$2450
- 2022 **Professional Development Grant**, SUNY ESF Graduate Student Association – \$50
- 2020, 2021 **Grober Graduate Research Fellowship**, SUNY College of Environmental Science and Forestry, Cranberry Lake Biological Station – \$14,300/year
- 2018, 2019 **Edward D. and Sally M. Futch Fellowship**, Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada – \$7,000/year
- 2019 **Student Travel Award**, American Ornithological Society – \$580
- 2019 **Student Membership Award**, American Ornithological Society – \$28
- 2018 **Student Travel Award**, North American Arctic Goose Conference – \$434

#### **AWARDS**

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- 2023 **Outstanding Doctoral Scholar Award**, Department of Environmental Biology, SUNY College of Environmental Science and Forestry
- 2021 **2019 Best Thesis Award**, School of Natural Resources, University of Missouri

#### **EXPERIENCE**

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- 2019 **Senior Research Technician**, University of Missouri  
*Columbia, MO* · 3 months
- Conducted Bayesian data analysis and prepared manuscripts.

- 2016 **Conservation GIS Lab Intern**, Smithsonian Conservation Biology Institute  
*Front Royal, VA · 6 months*
- Used R statistical software to analyze behavioral and physiological data.
  - Employed machine learning algorithms while working with large datasets to classify behavior from accelerometers.
- 2015-2016 **Hoofstock Behavior Research and Husbandry Intern**, Fossil Rim Wildlife Center  
*Glen Rose, TX · 9 months*
- Actively participated in design, performed behavioral observation, collected and organized video recordings, and maintained data for study on effects of GPS collars.
  - Assisted in and observed ungulate veterinary procedures, including capture and anesthesia.
  - Contributed to daily husbandry of a variety of ungulate species in a semi-natural pasture setting and smaller enclosures, and trained new staff member on routine.
- 2015 **Lead Volunteer Predator Research Technician**, The Cape Leopard Trust  
*Kamieskroon, Northern Cape, South Africa · 3 months*
- Provided fieldwork support for predator ecology and human-wildlife conflict project via daily physical and remote (VHF) trap checks and periodic cluster searches to identify kill sites and record vegetation data.
  - Participated in field work-ups of captured caracal (*Caracal caracal*), assisting in sample collection and data recording.
  - Deployed and managed trail cameras, reviewing photos in *Timelapse* software.
- 2014, 2015 **Northern Idaho Ground Squirrel Field Technician**, University of Idaho  
*Council, ID · 4 months/year*
- Conducted live-trapping, anesthesia, and PIT-tagging of squirrels and chipmunks.
  - Conducted vegetation surveys and maintained camera traps.
  - Located hibernacula via VHF telemetry.
- 2014 **Wildlife Rehabilitation Intern**, Sarvey Wildlife Care Center  
*Arlington, WA · 4 months*
- Assisted in daily husbandry of patients.
  - Developed skills in restraint and handling techniques of birds and mammals, as well as veterinary support skills.
  - Trained and directed volunteers in cleaning and feeding tasks.
- 2012-2014 **Research Assistant**, Cheetah Conservation Fund  
*Otjiwarongo, Otjozondjupa, Namibia · 2 years*
- Scat dog handler - responsible for car and maintenance training of two dogs, daily fieldwork, and designed database for data collection.
  - Trained interns and volunteers on cheetah (*Acinonyx jubatus*) husbandry and to give informational talks to visitors.
  - Compiled, cleaned, and analyzed data for 2011 and 2012 International Cheetah Studbooks.
  - Conducted various research or veterinary support tasks as assigned.

- 2011 **Intern**, Cheetah Conservation Fund  
*Otjiwarongo, Otjozondjupa, Namibia* · 3.5 months
- Managed data collection for camera traps and entered data.
  - Presented informational talks to the public and assisted in cheetah husbandry.

## TEACHING

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### SUNY College of Environmental Science and Forestry

- 2022 *Instructor* – Fundamentals of Bayesian Statistics (Spring semester, 9 students; graduate-level seminar)
- 2021 *Co-Instructor* – SMoREs-Statistical Modeling in R for Ecologists (Fall semester, 12 students; graduate-level)
- 2020 *Teaching Assistant* – Landscape Ecology (Fall semester, 15 students; Senior- and mainly graduate-level course)

### University of Missouri

- 2017, 2018 Teaching Assistant – Animal Population Dynamics and Management (Fall semester, 30 students; Senior- and graduate-level course)

### Miscellaneous

- 2016 Course Assistant – Spatial Ecology (2-week course, 20 conservation professionals; Smithsonian Conservation Biology Institute, *Front Royal, VA*)

## WORKSHOP ORGANIZATION

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- 2021 Biocultural Conservation and Public Engagement in Wildlife Biology, *The Wildlife Society Annual Conference, Half-day, Virtual* · Co-organizer
- 2018 Crash Course: Introduction to R Programming, *University of Missouri* · Organizer/Co-instructor

## OUTREACH

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### Presentations

- 2023 Using camera traps to study fishers. Virtual Presentation, MN 4-H Zooming into Wildlife
- 2022 Population Dynamics and Habitat Use in New York Fishers. *Virtual Presentation, Onondaga Audubon Monthly Program Meeting*
- 2021 Vital rates and habitat use in New York fishers. *Presentation, SUNY Oswego Zoological Student Association Meeting, Oswego, NY*
- 2019 Monitoring migration in arctic-nesting geese. *Presentation, Science on Tap, Columbia, MO*
- 2016 Conservation GIS. *Presentation, Smithsonian Conservation Biology Institute Autumn Conservation Festival, Front Royal, VA*

### Popular Article

- Cunningham, S. “Following Fishers in the North Country.” *New York State Conservationist*. Oct./Nov. 2022, pp. 16-19. [https://dec.ny.gov/docs/administration\\_pdf/consmag1022.pdf](https://dec.ny.gov/docs/administration_pdf/consmag1022.pdf)

## SERVICE

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- 2022 **Camp Fire Conservation Fund Professor of Wildlife Conservation Search Committee** – Graduate Student Representative
- 2019-present **Biocultural Conservation Institute** – Board Member-at-Large
- 2017-2019 **Wildlife and Fisheries Science Graduate Student Organization** – Member-at-Large, Vice President

## PROFESSIONAL SOCIETY MEMBERSHIP

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The Wildlife Society · Ecological Society of America · British Ecological Society  
*Formerly:* American Society of Mammalogists · American Ornithological Society

## SKILLS

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*Modeling and Analysis* Bayesian and likelihood statistical frameworks · Hierarchical models · Integrated population models · Machine learning

*Software and Programming* R · JAGS · Nimble · ArcGIS · MARK

*Fieldwork* Independent work · Lead/Supervisory roles · Remote locations · Scat dog handling · Veterinary support · Camera trap deployment · Live trapping (small carnivores, small mammals, waterfowl) · VHF telemetry · Vegetation surveys · Behavioral observations

## TRAININGS AND PROFESSIONAL DEVELOPMENT ACTIVITIES ATTENDED

- NIMBLE Virtual Short Course. 4-6 January 2023 (half days). *Virtual.*
- Presentation Matters. 6 November 2022 (half day). TWS Annual Conference, *Spokane, WA.*
- Fundamentals of Structured Decision Making. 2 October 2020 (full day). TWS Annual Conference, *Virtual.*