

The Pennsylvania State University

The Graduate School

**SPACE-USE AND MOVEMENT OF CANADA GEESE
IN RESPONSE TO HUNTING PRESSURE AND ANTHROPOGENIC LAND USE**

A Thesis in

Ecology

by

Karen Beatty Brzezinski

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The thesis of Karen Beatty Brzezinski was reviewed and approved by the following:

Frances E. Buderman
Assistant Professor of Quantitative Wildlife Ecology
Thesis Advisor

Jason Keagy
Assistant Research Professor of Wildlife Behavioral Ecology

Matthew R. Marshall
Adjunct Assistant Professor of Wildlife Conservation

Nathaniel R. Huck
Special Signatory
Waterfowl Biologist, Pennsylvania Game Commission

Jason Kaye
Distinguished Professor of Soil Biogeochemistry
Chair, Intercollege Graduate Degree Program in Ecology

ABSTRACT

The North American landscape has changed drastically over the last century through the conversion of wetlands, grasslands, and forests to intensive agriculture and urban development to meet human needs (Foley et al., 2005; Homer et al., 2020). Increased human use of the landscape affects wildlife's access to resources, behavior, and survival (Abraham et al., 2005; Bechet et al., 2004; Desrochers, 2010). Understanding wildlife behavior in relation to direct and indirect anthropogenic disturbance is necessary to develop appropriate and effective land use policies, management regulations, and conservation plans (Allen & Singh, 2016; McDuire et al., 2021). The direct effects of anthropogenic disturbance can result from human recreation activities, such as ecotourism, wherein species tend to increase vigilance, stress hormones, and flight distance when humans are present (Scheijen et al., 2021; Wolf & Croft, 2010). Anthropogenic disturbance affects wildlife indirectly through land conversion, which can disconnect habitats, thwart dispersal, and limit population size and range (Seaman et al., 2021). However, some species have managed to thrive in human-dominated landscapes, like waterfowl that take advantage of fallow croplands and turfgrass monocultures for reliable food sources (Washburn & Seamans, 2012).

For prey species, predation avoidance exerts a strong influence on behavior and space use. The landscape of fear describes an individual's cognitive map that incorporates perceived cyclical temporal and spatial variations in predation risk across the landscape (J. S. Brown & Kotler, 2004; Laundre et al., 2010). Further, the predation risk allocation hypothesis suggests that animals allocate feeding and anti-predator efforts variably in response to predation risk, trading-off between foraging and vigilance behavior based on perceived risk (Lima & Bednekoff, 1999). Prey species may also perceive some sources of anthropogenic disturbance as a component of the landscape of fear. For example, a grouse species in Europe (*Tetrao urogallus*) exhibited decreased activity in suitable habitats with higher levels of recreation (Rösner et al., 2014). For game species, hunters are part of an animal's landscape of fear. Hunting pressure has direct impacts on individuals through harvest and may have indirect impacts on behavior, such as changes in movement rates, habitat preference, and decreased foraging efficiency that reduces body condition (L. Brown et al., 2023; LeTourneux et al., 2021; Picardi et al., 2019). Hunting-

related changes in activity and space-use patterns have been documented in a variety of species and environmental settings. In ungulate populations, researchers have observed hunting-related increases in movement rates with no corresponding changes in habitat selection (C. L. Brown et al., 2020; Cleveland et al., 2012), and it has been suggested that the magnitude of response is related to variation in exposure to risk (Cromsigt et al., 2013). Many waterfowl species have also demonstrated measurable but inconsistent changes in landscape use and activity in response to hunting. For example, studies showed that hunting, whether from fixed (e.g., stationary blind) or mobile (e.g., boat) points prompted waterfowl to leave a site immediately but did not decrease overall abundance at the site (Bregnballe & Madsen, 2004; Madsen, 1998a). Providing waterfowl with access to undisturbed refuges has been identified as an effective management tool to buffer the effects of anthropogenic disturbance (Bregnballe et al., 2004; Madsen, 1998b), and waterfowl have been shown to move to refuges during the hunting season (Bechet et al., 2004; Roy et al., 2013).

Waterfowl's response to anthropogenic disturbance, including hunting, has been studied across a wide range of species and regions, often using direct observation or low-frequency tracking, which has limited the scope of inference (Beaumont et al., 2013; Bregnballe & Madsen, 2004; Roy et al., 2013). However, management of waterfowl remains a key focus of many hunter-affiliated conservation organizations and government agencies, and additional research using modern techniques is necessary for effective population management (Devers et al., 2017; U.S. Department of the Interior et al., 2018). Importantly, despite hunter retention and recruitment decreasing in recent decades, hunting remains a primary source of funding for state and federal wildlife conservation and management programs (Organ et al., 2012). In Pennsylvania, hunting-related purchases contribute one billion dollars to gross domestic product annually (Southwick Associates, 2021). Goose hunting in Pennsylvania accounts for a large portion of goose hunting in the eastern U.S. Geese (*Anser* spp and *Branta* spp.) harvested in Pennsylvania comprise approximately 20% of geese harvested within the Atlantic Flyway (R.V. Raftovich et al., 2021).

The Pennsylvania Game Commission operates Wildlife Management Areas, which are specifically managed to create hunting opportunities and increase game species by providing quality breeding and foraging habitat and undisturbed areas of refuge. Two management-related

goals of this study were to understand how resident Canada geese (*Branta canadensis*) move across the landscape during the hunting season and which habitat characteristics support nesting and foraging year-round, which can guide management decisions that maximize both goose abundance and hunting opportunities. Further, we aimed to expand our understanding of the landscape of fear by evaluating how this game species navigates the trade-off between threats and resources during the hunting season. By fitting resource selection functions and hidden Markov models to analyze fine-scale telemetry data from non-migratory geese that use carefully managed hunting areas, we will improve our understanding of Canada goose movement and habitat use with respect to hunting disturbance. The results will not only provide information about effective population management, but also provide insights into behavioral adaptations for predator avoidance.

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Chapter 1

Canada Goose Landscape Use in Response to Anthropogenic Disturbance

Introduction

Habitat selection is the result of an individual choosing where it spends time by balancing access to resources against predation risk (Boyce & McDonald, 1999; Fox & Madsen, 1997). Landscapes have changed drastically in the last century through land conversion: from wetlands, grasslands, and forests to intensive agriculture and urban development (Foley et al., 2005; Homer et al., 2020). Wildlife must adapt to changing land cover and habitat availability and quality, whether driven by natural seasonal changes or human alteration of the landscape (Hill & Frederick, 1997). Habitat quality is often inferred from the way individuals distribute themselves across the landscape (M. D. Johnson, 2007), and land management decisions are often based on inferred habitat quality, which assumes that individuals exclusively select habitats that increase their fitness (Chalfoun & Martin, 2007).

Areas where an animal rests, feeds, and cares for young constitutes its home range, which can shift seasonally with life history or resource availability (Burt, 1943). Often, several habitat types are needed throughout an animal's lifespan to fulfill its needs (M. D. Johnson, 2007). For example, elk (*Cervus canadensis*) have been shown to shift habitat use daily and seasonally in sync with activity patterns and life history cycle (Roberts et al., 2017). In addition to an individual's habitat needs changing over time, resource availability can also change. For example, the depletion of food resources throughout a season is thought to have caused snow geese (*Anser caerulescens*) to shift their roosting sites to be closer to more plentiful food (Hill & Frederick, 1997). Researchers often estimate home ranges to understand how animals position themselves among resources (Powell & Mitchell, 2012; Signer et al., 2015). Knowing home range boundaries can elucidate where an animal chooses to be on the broad landscape (e.g., situated in relatively high elevations) and can be used alongside methods like resource selection functions to determine which resources an animal uses within its home range (Gigliotti

et al., 2023; Powell & Mitchell, 2012). Researchers can also compare home range boundaries between seasons and among individuals to determine what causes an animal to shift its home range (C. L. Brown et al., 2020). As resource needs and resource availability fluctuate, individuals assess trade-offs of several habitat options when choosing where to spend time (Chalfoun & Martin, 2007; McGarigal et al., 2016).

Like the effects of resource availability, extrinsic factors that deter habitat use can cause temporal shifts in activity. For example, lions (*Panthera leo*) were shown to avoid areas with human activity during the day but feed near humans at night, when human activity was reduced (Suraci et al., 2019). For prey species, predation avoidance exerts a strong influence on space-use via the landscape of fear, which is an individual's cognitive map that incorporates predation risk (J. S. Brown & Kotler, 2004; Laundre et al., 2010). For example, Dorak et al. (2017) found that Canada geese (*Branta canadensis*) may choose to winter in urban areas with low-quality forage to minimize predation risk. Like the lions above, researchers found that elk synchronized their daily behavior patterns with wolf activity and used riskier areas when wolves were less active (J. S. Brown & Kotler, 2004). Similarly, the grey partridge (*Perdix perdix*) appeared to adjust its habitat use in ways that reduced predation risk at night and reduced exposure to hunting pressure during the day (Harmange et al., 2021). How animals use the landscape is dictated by how they navigate both food resources and predation risk (Gallagher et al., 2017).

Anthropogenic activities can modify how wildlife perceive the risks and rewards associated with available habitat, which may affect their spatial distribution. For game species, hunters are part of an animal's landscape of fear (L. Brown et al., 2023). Hunting-related changes in space-use patterns have been documented in a variety of species and environmental settings. In some ungulate populations, individuals shifted their home range and habitat use during the hunting season (Rhoads et al., 2013; Spitz et al., 2019). Avian game species have also been shown to modify their foraging behavior in relation to hunting. During the hunting season, northern bobwhite (*Colinus virginianus*) altered the timing and duration of foraging (McGrath et al., 2018), and snow geese (*Anser caerulescens*) used lower-quality foraging habitats that likely contributed to reduced body condition (Bechet et al., 2004).

The Pennsylvania Game Commission (PGC) operates Wildlife Management Areas (WMAs), which are specifically managed to create hunting opportunities and increase game

species by providing quality breeding and foraging habitat and undisturbed areas of refuge. The PGC manages a robust population of resident Canada geese on certain WMAs by customizing vegetative cover types and reducing hunting pressure through shorter hunting seasons and lower bag limits compared to elsewhere in the commonwealth (Lau & Yeager, 2021). Additionally, the number of hunters on these WMAs is restricted through a lottery system and to stationary blinds located within a 3.5 square mile area.

Understanding how hunting affects target species is necessary to effectively manage WMAs. Waterfowl have been shown to move to disturbance-free refuges during the hunting season (Bechet et al., 2004; Roy et al., 2013). In one study, Canada geese were observed shifting long distances (>40km) from areas of high to low hunting pressure in the weeks leading up to and during the start of hunting season (Beaumont et al., 2013; Dieter et al., 2010). In addition to spatial refuge in hunting areas, temporal refuge during the hunting season has been tested at varying scales. Studies at two different sites found that neither decreasing the duration of a temporal refuge from two weeks to one week, nor increasing a temporal refuge from two days to four days changed overall duck abundance at the study sites (Bregnballe & Madsen, 2004; St James et al., 2013). Dooley et al. (2010) found that mallards (*Anas platyrhynchos*) returned to an area within one to two days post-disturbance, and that individuals tended to return to areas of previous use rather than abandon them for unknown areas.

While the use of refuges is of particular interest in waterfowl research, recent studies have also evaluated habitat selection in relation to hunting seasons. Animals may trade-off feeding and anti-predator efforts, which could involve altering habitat selection to avoid predation risks like hunting (Lima & Bednekoff, 1999). Studies have shown that this trade-off in snow geese may negatively affect body condition and subsequently breeding success (LeTourneux et al., 2021). Mallards in Illinois used areas open to hunting much more than areas closed to hunting, and were more often observed in open water, followed by corn, then herbaceous habitats, but comparisons were not drawn between hunting and non-hunting time periods (Yetter et al., 2018). In a similar study, Canada geese spent much more time in areas closed to hunting and were more often observed in 'natural' areas than agricultural habitats, but again comparisons with non-hunting time periods were not made (Beaumont et al., 2013). Comparing habitat selection between hunting and non-hunting periods can more reliably indicate whether desirable

resources are being sacrificed, especially when the objective involves quantifying the effect of hunting (LeTourneux et al., 2021).

The primary goal of this study was to understand how hunting activity affects the resource selection of a game species. We also aimed to understand how resource selection of the species changes throughout the breeding season. Understanding resource selection in both contexts can collectively guide management decisions to maximize goose abundance and hunting opportunities. We analyzed fine-scale telemetry data from non-migratory Canada geese that use carefully managed hunting areas to understand habitat selection by a) determining whether geese used the WMAs less when hunting was occurring on the sites, b) evaluating how goose resource selection changed in response to hunting disturbance on the WMAs, and c) evaluating how goose habitat preferences varied with life history stages, particularly during the breeding season. We hypothesized that geese would partition their habitat selection either spatially or temporally to avoid hunting pressure (Bechet et al., 2004; McGrath et al., 2018).

Methods

Study Area

The study occurred at two Pennsylvania Wildlife Management Areas specifically managed for waterfowl: Pymatuning WMA and Middle Creek WMA, hereafter referred to as Pymatuning and Middle Creek. Pymatuning is 9,661 acres located in Crawford County in northwestern Pennsylvania (41.591816, -80.409158), and Middle Creek is 6,207 acres located in Lancaster and Lebanon Counties in southeastern Pennsylvania (40.271050, -76.249455). Pymatuning is comprised of croplands, wetlands, and 1,600 acres of an 17,088-acre reservoir, and the surrounding area is a patchwork mixture of agriculture and deciduous forest. Pymatuning abuts Pymatuning Reservoir and Pymatuning State Park. Middle Creek is comprised of croplands, deciduous forest, and an approximately 400-acre lake, and the surrounding area is primarily agriculture with low density development and interspersed deciduous forest. Pymatuning and Middle Creek are sectioned into Public Hunting Areas

(hunting allowed during open seasons), Controlled Hunting Areas (hunting allowed on specific days with special permits; CHA), Public Recreation Areas (hunting allowed except for waterfowl), and Propagation Areas (closed to entry). Because of the large number of waterfowl using these lands, hunting at Pymatuning and Middle Creek WMAs is highly desirable, and access to PGC-maintained blinds in CHAs is permitted via a lottery system. Details about the hunting regulations at both WMAs is provided in Table 1-1. Hunting is allowed from 05:00 to 12:30 at Pymatuning and 05:00 to 13:30 at Middle Creek to coincide with the times of day when geese are moving between overnight roosting sites and morning feeding sites and thus could be lured into a hunter's spread. In Pennsylvania the primary threat to an adult Canada goose is hunting. As of 2018, Crawford, Lancaster, and Lebanon Counties ranked 6th, 1st, and 7th out of 67 counties for goose harvest in the Commonwealth, and 72nd, 24th, and 160th out of 3,115 counties for goose harvest in the U.S., respectively (U.S. Fish and Wildlife Service, 2018). During the state-wide Canada goose hunting season, hunting is also allowed in areas outside the WMAs, including land immediately adjoining the properties. The state-wide hunting regulations are less restrictive than the WMA-specific hunting regulations, and state-wide hunting occurs during the same general timeframe as the WMA hunting seasons (Lau & Yeager, 2021).

Table 1-1: Canada goose hunting regulations at Pymatuning and Middle Creek Wildlife Management Areas.

Wildlife Management Area	No. Hunting Blinds	Hunting Days	Hunting Periods	Bag Limits †	
Pymatuning	36	Mo We Fr Sa	2021	CHA: 1 per day	
					Oct 23-Nov 24
					Dec 20-Feb 12
			2022		
			Oct 29-Nov 25		
			Dec 12-Jan 14		
Middle Creek	2021	Tu Th Sa	2021	CHA: 1 per season	
	26				Nov 23-Nov 25
	2022				Dec 28-Jan 22
	25		2022		
			Nov 22-Nov 24		
			Dec 24-Jan 21		
† Controlled Hunting Area (CHA) Source: (Lau & Yeager, 2021)					

Field Methods and Tracking

We trapped geese during their annual flightless molt period on June 23 and 24, 2021, and June 24 and 28, 2022. Geese were gradually herded into pens (i.e., drive-trapping), sexed via cloacal inversion, and aged as hatch-year or after-hatch-year (AHY) based on feather characteristics. Female AHY geese were marked with a uniquely numbered aluminum U.S. Geological Survey Bird Banding Laboratory leg band and fitted with a remotely programmable solar-powered Global Positioning System - Global System for Mobile Communications (GPS/GSM) receiver attached around the neck (Ornitela OrniTrack-N44 4G, Vilnius, Lithuania). The neck collars weighed approximately 44 grams, which is about 1.5% of a typical individual's body weight, and were assumed to not inhibit natural movement and behavior. We marked only female AHY geese to avoid replication from collaring both individuals in a mated pair and to ensure that each goose had experienced at least one hunting season prior to the study. We marked 68 geese during 2021 and an additional 66 geese during 2022. During the 2022 trapping effort, three geese were recaptured to replace their GPS collars and one goose was recaptured to replace its leg band. Total handling time per goose was 5-10 minutes, and geese were released at the capture location. All geese were captured and handled using methods approved by the Pennsylvania State University Institutional Animal Care and Use Committee (protocol no. 202001718). The GPS receivers recorded a bird's location, altitude, velocity, and triaxial acceleration every 10 minutes. Data were uploaded to the web-based Movebank platform twice a day using the 4G GSM network (Wikelski et al., 2023).

Data Processing

Data were downloaded from Movebank (Kays et al., 2022) and processed and analyzed using R (R Core Team, 2022). Locations were collected in both the World Geodetic System 1984 (WGS84) and Universal Transverse Mercator (UTM) coordinate reference systems, and we used UTM Zone 17 and 18 location data for Pymatuning and Middle Creek WMA, respectively. Locations with a horizontal dilution of precision value greater than 2.0 were removed from the sample due to presumed low accuracy (Specht, 2022). For each bird, location

records with duplicated timestamps (n=900) were removed, and the duplicate record containing metadata was retained. Date-time stamps were transformed to local time using the *'lubridate'* package in R to account for daylight savings time (Garrett Grolemond & Hadley Wickham, 2011). Observations were filtered to legal hunting hours at each WMA (Pymatuning: 05:00-12:30, Middle Creek: 05:00-13:30). Locations greater than 100 meters above a site's average surface level and with a speed greater than 4 meters per second were omitted under the assumption that birds within 100 meters of the ground moving relatively slowly were choosing to use an area and not flying over it.

Because hunting occurs at seasonal and daily timescales, we analyzed space-use at both coarse and fine spatial and temporal scales. For a coarse-scale analysis, we limited observations to locations marked within seven miles of the boundary of each WMA during the respective on-WMA hunting season (i.e., hunting periods plus the mid-season non-hunting 'split' period) plus seven days before and after. We buffered the WMA by seven miles for this analysis because birds that were observed both on and off the WMAs typically remained within seven miles of the WMA, indicating that birds within this range were choosing to use or not use the WMA at any given time. We resampled the observations to occur at 60-minute intervals using the *'amt'* package (Signer et al., 2019). For a fine-scale analysis, we limited the observations to locations observed within the boundary of each WMA during the WMA-specific hunting periods plus one day before and after (Table 1-1, Figure 1-1) (D. Jones, personal communication, 14 Feb 2022). At this scale we excluded the mid-season non-hunting 'split' period, which is a several-week period during which hunting is not allowed on the WMAs. Excluding the non-hunting 'split' period allowed us to directly compare hunting and non-hunting days during the on-WMA hunting season and evaluate whether geese perceived the pattern of hunting pressure on a daily cycle. We conducted two analyses at the fine scale: one used data from both WMAs (hereafter referred to as "two-site fine scale") and the other used data from only Middle Creek (hereafter referred to as "Middle Creek fine scale") to make use of higher resolution environmental data available exclusively for that site.

Covariates

We modeled habitat selection using covariates representing environmental resources, risks, and conditions listed in Table 1-2 to estimate the relative probability of an individual selecting for or against certain environmental characteristics (Matthiopoulos et al., 2015). Hunting day on-WMA was determined from the Hunter's Digest and WMA managers (C. Deal, personal communication, 12 Aug 2022; L. Ferreri, personal communication, 2 Sep 2022), and hunting period on-WMA was derived from hunting days and constitutes a consecutive period of alternating hunting and non-hunting days (Table 1-1, Figure 1-1). Hunting intensity was represented by number of hunters as recorded by PGC staff during hunter check-in (C. Deal, personal communication, 28 Feb 2022 and 24 Feb 2023; S. Ferreri, personal communication, 8 Feb 2022; B. Collett, personal communication, 17 Feb 2023). We chose 'number of hunters' to represent hunting intensity because the value was independent of goose presence near a blind, whereas the number of harvest attempts was conditional on goose presence (i.e., a hunter would only fire shots if a goose was within range). The number of hunters and number of harvest attempts were correlated ($r=0.71$), but the number of hunters was able to represent the amount of hunting intensity at a site on a given day without being confounded by goose activity. Larger values indicate more hunters on a given day and thus represent a higher hunting intensity. At Middle Creek, the records of hunting intensity were maintained on a per-blind per-day basis; therefore, for the two-site fine-scale analysis we aggregated the daily metrics across the entire WMA to match the resolution of the data available from Pymatuning WMA. For the Middle Creek fine scale analysis, we calculated hunting intensity for each observation by multiplying the number of hunters at each blind by the inverse distance between each blind and each observed location and averaging across the two nearest blinds, such that a larger value indicates that an observation is located very close to more hunters, a mid-range value could indicate that an observation is located closer to fewer hunters or farther from many hunters, and a small value indicates that an observation is located farther from relatively few hunters. The maximum number of hunters per blind was four. Daily weather data were obtained from Weather Underground's KPALINES8 and KPANEWMA19 weather stations for Pymatuning and Middle Creek, respectively (The Weather Channel Product and Technology, n.d.). We chose to include

daily low temperature and total daily precipitation when fitting the models based on species life history, a known tendency to seek open water during periods of extreme cold and precipitation, and a tendency to use different food sources depending on wetness (N. Huck, personal communication, 18 Jan 2023). Habitat was delineated using the USGS National Land Cover Dataset (2019), projected from a 30-meter resolution to a 10-meter resolution, and aggregated into five functional habitat categories: open water, grass, crop, forest, and developed (Jon Dewitz & U.S. Geological Survey, 2021). Distance from open water was calculated at a 10-meter resolution derived from the NLCD-derived habitat data layer. Similarly, distance from hunting blind was calculated at a 10-meter resolution derived from blind point locations provided by WMA managers (C. Deal, personal communication, 4 Feb 2022; S. Ferreri, personal communication, 8 Feb 2022; L. Ferreri, personal communication, 5 Sep 2022). Vegetative cover at Middle Creek was delineated and provided by the WMA managers as a shapefile with the following categories: row crop (corn, wheat, or rotational hay), warm season grass, cool season grass, old field reverting (equivalent to warm season grass), food plot (equivalent to cool season grass), or hedgerow (equivalent to forest) (S. Ferreri, personal communication, 19 Oct 2022). We used these primary categories to delineate vegetative cover, but we used the row crop subcategories to delineate the crops by type. The verified vegetative cover data were only used for the Middle Creek fine-scale analysis because Pymatuning did not have ground-truthed land cover data at a comparable resolution. The Middle Creek fine-scale model substituted the verified vegetation cover data for the NLCD data where possible because the ground-truthed data did not cover the full WMA (the ground-truthed data did not include delineations of forested, developed, and open water areas), which resulted in a blend of habitat types from both data sources. In all three models, continuous variables were standardized to have a mean of zero and a standard deviation of one. To assign covariate values to each data point, we either extracted the spatial covariate values directly from the raster layers via the *'raster'* package in R (Hijmans, 2023) or assigned non-spatial data to an observation by matching the timestamp dates.

Table 1-2: Model covariates included in resource selection functions.

Variable	Description
On WMA	Goose location is outside (0) or within (1) the boundary of a WMA
Site	Pymatuning WMA (0) or Middle Creek WMA (1)
Hunting day on-WMA	Day when Canada goose hunting is (1) or is not (0) allowed in the WMA Controlled Hunting Areas
Hunting period on-WMA	Span of days that contains alternating hunting and non-hunting days on the WMA (1) or span of non-hunting days between two hunting periods (0)
Number of Hunters ^	Daily total number of hunters on the WMA (two-site model) or Number of hunters per blind per day averaged across the two nearest blinds to each observation and weighted by the inverse distance from each blind (Middle Creek model)
Habitat	Land cover type categorized as open water, grassland, cropland, forest, or developed
Cover	Land cover type verified by Pennsylvania Game Commission staff categorized as corn, wheat, hay, cool season grass mix (includes food plots), warm season grass mix (includes reverting fields), and hedgerow (incorporated into forest category)
Distance from open water ^	Distance (m) to nearest habitat categorized as open water
Distance from hunting blind ^	Distance (m) to nearest hunting blind
Low temperature ^	Lowest temperature (°F) recorded at the nearest weather station on a given day
Precipitation ^	Total amount (in) of daily rainfall or snowfall
^ Value range was standardized (scaled and centered) to have a mean of 0 and standard deviation of 1. Note: Distances are calculated in meters, temperature is measured in °F, and precipitation is measured in inches.	

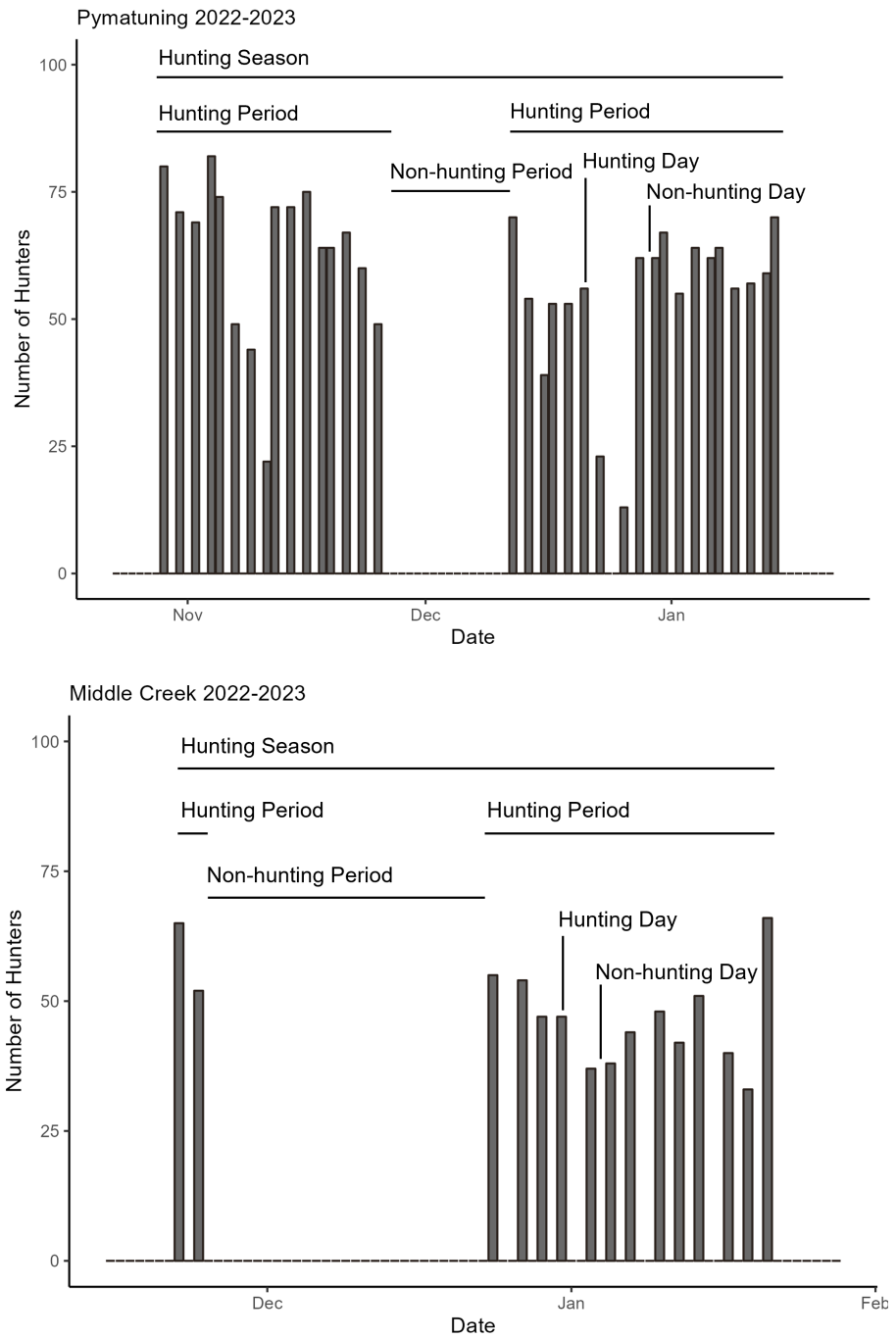


Figure 1-1: On-WMA hunting days and periods at Pymatuning and Middle Creek during the second study season depicted by number of hunters.

Resource Selection During Hunting Season

To understand how goose habitat selection changed in response to hunting disturbance on the WMAs, we fit a use-availability resource selection function (RSF) to model second-order habitat selection by quantifying the relative probability of use of habitat types within the study area (Avgar et al., 2017; Boyce et al., 2002; Manly et al., 2002; Northrup et al., 2022). We quantified the habitat characteristics at an individual's observed location (used) in proportion to the habitat characteristics on the entire WMA or beyond (available) (D. H. Johnson, 1980). To generate the available locations, we used the '*sf*' package in R to create random points at a ratio of 10 available points per 1 observed point (Pebesma, 2018). While there is no consensus on a standard multiplier of the number of used locations for the availability sample, studies have suggested that a multiplier between 10 and 50 is likely sufficient for a robust analysis (Fieberg et al., 2021; Northrup et al., 2013). We believe the 1:10 ratio was sufficient to neither under-sample the available habitat nor overlap used and available points (Keating & Cherry, 2004; Northrup et al., 2013). We assigned covariate values to each available point after assigning the timestamp and individual identifier of each observed point to 10 available points.

We fit generalized linear mixed effects models (GLMMs) using a logit link to approximate the exponential form of an RSF. We included individual identifier as a random intercept to account for reference class preference within individuals and unbalanced sample sizes among individuals (Gillies et al., 2006; Muff et al., 2020). We fit the models using the '*glmmTMB*' package in R and set the variance to 10^6 to avoid the individual intercept parameters from being shrunk towards the overall mean (Brooks et al., 2017; Muff et al., 2020). A basic tenet of resource selection is that an individual could relocate to any location within the study area during each sampling interval (Matthiopoulos et al., 2015). Hence, at each time step, the individual is selecting their current location from all possible locations in the study area. If this is not true, and if movement is more restricted, then the general recommendation is to use a step-selection function (SSF, or a conditional habitat selection model) as opposed to an RSF. Our data show that geese can travel at a rate of at least five to twelve miles per ten minutes, which means an individual could fly between the farthest extents of each WMA (approximately 9.5 miles at Pymatuning and 6.5 miles at Middle Creek), or from anywhere within the 7-mile

buffered area onto the WMA, within our 10-minute sampling interval and therefore our data meet the relocation assumption for the fine-scale analyses and coarse-scale analysis, respectively. A summary of the resource selection models is provided in Table 1-3.

Coarse Scale

At the coarse spatial scale we fit two models to evaluate selection of the WMA at fine and coarse timescales. In the first model, to evaluate selection at a finer timescale, we modeled selection as a function of the WMA (reference category is areas off the WMA). We allowed for an effect of hunting day and an interaction between hunting day and the WMAs. In the second model, to evaluate selection at a coarser timescale, we modeled selection as a function of the WMA and allowed for an effect of hunting period and an interaction between hunting period and the WMAs. In both cases the main effect of the WMA provides inference for relative selection for being on the WMA during a non-hunting day or period. The main effect of hunting day or period provides inference for how relative selection of areas off the WMA (the reference) changes during a hunting day or period. The interaction provides inference for how selection of areas on the WMA changes during a hunting day or period relative to the reference (i.e., selection for areas on the WMA may be additionally modified beyond the main effect of hunting day/period). Because we studied a resident population, we predicted that the geese would prefer to be on the WMAs when no hunting was happening. Additionally, because prior waterfowl studies have shown that birds temporarily abandoned hunted areas and returned to known areas instead of novel areas (Dooley et al., 2010), we predicted that geese would avoid the WMAs during hunting days, but would not avoid the WMAs during hunting periods.

Two-Site Fine Scale

At the fine scale, we modeled selection as a function of habitat type (reference category was open water) and distance from hunting blind. The main effects of habitat refer to selection of each type on non-hunting days when the distance from water, precipitation, and temperature

were all at their average values for the study period (zero on the standardized scale). The main effect of distance from blind provides inference for how relative selection for each one-standard deviation increase in distance from the nearest hunting blind changes on a non-hunting day.

We allowed for an effect of hunting day and an interaction between it and habitat type and distance from hunting blind. The main effect of hunting day provides inference for relative selection of open water on a hunting day. The interactions between habitat and hunting day adjusts the habitat selection strengths to represent relative selection on hunting days. The interaction between distance from blind and hunting day adjusts the selection strength for distance from blind to represent relative selection on a hunting day.

We also allowed for interactions between distance from water and hunting day and distance from water and habitat type, to allow habitat preference to vary depending on proximity to water. The main effect of distance from water was excluded because it is confounded with the open water habitat type. As described previously, the main effects of habitat would refer to selection of each type on non-hunting days when the distance from water, precipitation, and temperature were all at their average values for the study period (zero on the standardized scale). The interaction with distance from water represents the additional effect of every one-standard deviation increase in distance from water in each habitat type. The interaction between distance from water and hunting day represents the additional effect of each one-standard deviation increase in distance from water on a hunting day.

We allowed for interactions between habitat and total daily precipitation and habitat and daily low temperature, to allow habitat preference to vary depending on weather. The main effects of precipitation and low temperature, for which the other covariate values are the same across the WMA on a given day, represent how a one-standard deviation increase in precipitation or temperature affects the relative selection for open water. The interaction terms represent how relative selection for each habitat type varies with weather.

Lastly, we allowed for an interaction between distance from hunting blind and number of hunters. As described previously, the main effect of distance from blind provides inference for how relative selection for each one-standard deviation increase in distance from the nearest hunting blind changes on a non-hunting day when there are no hunters on the landscape. Likewise, the main effect of number of hunters represents how each one-standard deviation

increase in number of hunters on the WMA modifies relative selection of open water (the reference). The interaction term represents how the relative selection of a location further changes with each one-standard deviation increase in distance from hunting blind given a certain number of hunters (i.e., the magnitude of the effect of distance to blind changes depending on the number of hunters).

Because prior studies found that waterfowl seek refuge during hunting (Beaumont et al., 2013; Bechet et al., 2004; Roy et al., 2013), and most hunting blinds were located in grassland (n=28) or cropland (n=27) away from water, we predicted that preference for water would increase on hunting days and preference for grassland and cropland would decrease on hunting days. However, because hunting blinds were deliberately located in appealing habitat, we predicted that geese would demonstrate a preference for being closer to blinds on non-hunting days and a preference for being farther from blinds on hunting days. Additionally, we predicted that as the number of hunters increased the preference for being closer to blinds would decrease.

Middle Creek Fine Scale

We fit the Middle Creek fine-scale model using the same model structure as the two-site fine-scale model with one substitution: the blended vegetation cover and NLCD data to represent habitat types. Like the two-site fine-scale model, we predicted that preference for water would increase on hunting days because hunting mostly took place away from waterbodies which would then serve as a refuge (Beaumont et al., 2013; Yetter et al., 2018). Because most blinds were located in cool grasslands (n=7) and corn (n=7), we predicted that relative preference for cool grass and corn would decrease on hunting days. We predicted that geese would demonstrate a preference for being closer to blinds on non-hunting days and a preference for being farther from blinds on hunting days and as the number of hunters increased. Because of the high-resolution hunting and land cover data, we also expected to see more nuance in habitat preference and avoidance, especially among the crop and grassland types. More hunting blinds were located in cool grasslands and corn than wheat (n=3) and hay (n=3), so we predicted that geese would show stronger relative avoidance of cool grass and corn than wheat and hay on hunting days.

Home Range Estimation

To determine whether geese abandon the WMAs during hunting and evaluate whether space-use changes in response to hunting pressure, we estimated and compared individual home ranges during the on-WMA hunting season and the proportion of observations documented on the WMA. While biologists have proposed many definitions of home range (Burt, 1943; Fleming et al., 2015), the definition applied during any given study should reflect the research questions and objectives of that study and the life history of the study species (Börger et al., 2006). For our purposes, home range is most appropriately defined as an individual's cognitive map, which includes locations of travel routes, food, shelter, predation threats, and breeding resources (Laundré et al., 2001; Powell & Mitchell, 2012). Additionally, we were interested in estimating and comparing the boundaries of where individuals were observed. Thus, our definition of home range most closely aligns with what has been deemed an 'occurrence distribution' as opposed to a 'range distribution' (Fleming et al., 2015; Signer & John R. Fieberg, 2021).

There are numerous home range estimation methods at our disposal, and methods that estimate home range using utilization distributions (UDs) are typically better suited to GPS-derived location data (Walter et al., 2015). While several recent studies of goose space use employed the Brownian bridge movement model (BBMM) (Dorak et al., 2017; Zheng et al., 2018), we chose kernel density estimation with reference bandwidth (KDE_{href}) via the '*adehabitatHR*' package (Calenge, 2006) because short interval data points have been shown to yield well-estimated UD via kernel estimators (Kie et al., 2010). Furthermore, several studies have shown that choosing a sufficient sample size and rate, and biologically relevant analysis period is equally important as choice of estimator when the goal is comparison among home ranges (Signer et al., 2015; Signer & John R. Fieberg, 2021).

We used the 95 percent probability contour of the UD to represent home range. We retained observed locations within seven miles of the WMAs for both the coarse- and fine-scale analyses. Unlike the RSFs, we did not exclude locations based on speed or altitude because we included travel routes in our definition of home range. At the coarse scale, we compared estimated home ranges between the on-WMA hunting periods (150 days at Pymatuning, 61

days at Middle Creek) and the non-hunting 'split' period (41 days at Pymatuning, 61 days at Middle Creek). At the fine scale, we compared estimated home ranges between hunting days (84 days at Pymatuning, 28 days at Middle Creek) and non-hunting days (67 days at Pymatuning, 33 days at Middle Creek) during the on-WMA hunting periods. We inferred shifts in home range by calculating percent overlap between each individual's hunting and non-hunting home ranges as a ratio of overlap area to non-hunting home range area (Fieberg & Kochanny, 2005; Kernohan et al., 2001). To estimate whether home range sizes changed (i.e., contracted or expanded), we calculated the ratio of home range size during hunting to home range size during non-hunting. We also compared mean home range sizes between hunting and non-hunting using paired t-tests and fit linear mixed models using the *lme4* package (Bates et al., 2015) with home range size as the response variable, hunting day or period as a fixed effect, and individual as a random effect. To evaluate whether geese were abandoning the WMAs during hunting, we calculated the proportion of observed locations on the WMAs during hunting and non-hunting days and periods. If we expect geese to abandon the WMAs on hunting days, but return on non-hunting days and not abandon the WMAs throughout the hunting periods (Bregnballe & Madsen, 2004; Dooley et al., 2010), then we should see larger home ranges on hunting days than non-hunting days and equal home ranges between hunting periods and non-hunting periods. Thus, at the coarse scale of analysis, we predicted that the amount of non-hunting period home range also used during the hunting period would be greater than 50 percent, the ratio of hunting period home range size to non-hunting period home range size would be approximately 1, the home range sizes would not be significantly different between the hunting and non-hunting periods, the effect size of hunting period would be approximately zero, and the proportion of observations on the WMAs would be greater than 70 percent. At the fine scale of analysis, we predicted that the amount of non-hunting day home range also used during hunting days would be less than 50 percent, the ratio of hunting day home range size to non-hunting day home range size would be greater than 1, the home range sizes would be significantly different between hunting and non-hunting day, the effect size of hunting day would be greater than zero, and the proportion of observations on the WMAs would be less than 50 percent on hunting days but greater than 50 percent on non-hunting days.

Resource Selection During Breeding Season

To evaluate how goose habitat preferences vary seasonally with life history stages, we modeled habitat selection during the breeding season using the same methods as for hunting season. We fit a use-availability RSF to model second-order habitat selection with a 1:10 ratio of used to available locations (Avgar et al., 2017; Boyce et al., 2002; Manly et al., 2002; Northrup et al., 2022). We used the *'glmmTMB'* package in R to fit generalized linear mixed effects models using a logit link to approximate the exponential form of an RSF and a random effect of individual (Brooks et al., 2017; Muff et al., 2020).

For this analysis we included locations observed from March through August and divided them into three breeding phases of adult females: nesting (April), with goslings (May 15 – June 15), and fledged offspring (August) (N. Huck, personal communication, 14 Jun 2023). We included locations documented between 05:00-10:00 and 16:00-21:00, when geese are typically more active. We fit this model using observations within the WMA boundaries. To account for less movement by breeding females during the breeding season, we resampled the observations to occur at 60-minute intervals using the *'amt'* package (Signer et al., 2019). A summary of the resource selection models is provided in Table 1-3.

Two-Site

We modeled selection throughout the breeding cycle as a function of habitat type and distance from water. We fit a separate model for each breeding phase. Within each model, the effects of habitat refer to relative selection of each type relative to the reference habitat type (i.e., open water). The effect of distance from water provides inference for how relative selection changes with each one-standard deviation increase in distance from water. Because crops are not a prominent food source during the breeding season, we predicted that geese would show preference for grassland and open water relative to all other habitat types throughout the three phases. Additionally, we predicted a relative preference for developed areas during the gosling phase because of a tendency for geese to feed in the maintained grasses around buildings, parking lots, and roadsides.

Middle Creek

We also fit a breeding season resource selection function to the Middle Creek data to take advantage of the high-resolution land cover data available exclusively for that site. As with the hunting season Middle Creek model, we substituted the blended vegetation cover and NLCD data to represent habitat types. We fit a separate model for each breeding phase and structured the models in the same way as the two-site models. Like the two-site model, we predicted that geese would show preference for cool grasslands and open water relative to all other habitat types because warm grasslands and all three croplands are not a typical food source during the breeding season. We also predicted a relative preference for developed areas during the gosling phase.

Table 1-3: Summary of resource selection function models.

Model Name	Model Formula
Hunting Season	
Coarse Scale	
Coarse Timescale	Used $\sim (1 id) + on\ WMA * hunt\ period$
Fine Timescale	Used $\sim (1 id) + on\ WMA * hunt\ day$
Fine Scale	
Two-Site	Used $\sim (1 id) + habitat + precip + low\ temp + hunt\ day + dist\ blind + num\ hunters + habitat : dist\ water ^ + habitat : precip + habitat : low\ temp + habitat : hunt\ day + dist\ water : hunt\ day + dist\ blind : hunt\ day + dist\ blind : num\ hunters$
Middle Creek	Used $\sim (1 id) + cover + precip + low\ temp + hunt\ day + dist\ blind + num\ hunters + cover : dist\ water ^ + habitat : precip + habitat : low\ temp + habitat : hunt\ day + dist\ water : hunt\ day + dist\ blind : hunt\ day + dist\ blind : num\ hunters$
Breeding Season	
Two-Site	Used $\sim (1 id) + habitat + dist\ water + breeding\ phase$
Middle Creek	Used $\sim (1 id) + cover + dist\ water + breeding\ phase$
^ Does not include an interaction between open water habitat type and distance from water.	

Results

We collected 7.4 million observed locations from 134 geese, of which up to 210,302 locations from 121 geese were included in the final hunting season analyses after filtering the data as described in the Methods – Data Processing section above (Table 1-4). The breeding season analyses included 178,006 observations of 64 geese at Pymatuning and 166,508 observations from 67 geese at Middle Creek.

Table 1-4: Number of tracked geese and observation records collected during the study and included in hunting season analyses.

WMA	Total		Coarse-scale Analysis		Fine-scale Analyses	
	Number of Geese	Number of Observations	Number of Geese	Number of Observations	Number of Geese	Number of Observations
Pymatuning	66	4,034,155	54	49,547	48	151,743
Middle Creek	68	3,374,444	38	28,810	33	58,559
Total	134	7,408,599	92	78,357	81	210,302

Interpretation of Model Effects

The models were fit using effects parameterization, meaning the estimated parameter represents the added effect of that parameter in relation to a reference category. The direction and magnitude of each parameter estimate indicates the log relative strength of selection for or against that covariate. To ease interpretability, we can exponentiate the coefficients to determine the relative selection strength of each fixed effect, where a value greater than one indicates relative selection for a feature and a value less than one indicates relative selection against a feature (Fieberg et al., 2021). When not exponentiated, the coefficient (β) represents the log relative selection strength (logRSS) of that parameter, where a positive value indicates relative selection for a feature and a negative value indicates relative selection against a feature. We drew inference from the coefficient of each estimated parameter and its 98% confidence interval. We chose this relatively large confidence interval because the exceptionally large

quantity of available data resulted in low levels of parameter uncertainty. For continuous predictors (e.g., distance from blind), the exponentiated coefficient quantifies the relative selection of locations that differ by 1 standard deviation (SD) of the predictor (because the continuous predictors were standardized). For categorical predictors (e.g., developed habitat), the exponentiated coefficient quantifies the relative selection of developed locations relative to the reference category (in this case, open water) when all other predictor values are held constant. For example, the estimated coefficient for developed land in the two-site fine-scale model is -7.41, which means geese were 0.0006 times as likely to select for developed land than open water ($\exp(-7.41)$), or, inversely, that geese were 1,652 times as likely to select for open water than developed land ($\exp(|-7.41|)$) on non-hunting days when the distance from water, precipitation, and temperature were all at their average values for the study period (i.e., zero on the standardized scale). The estimated coefficient for distance from blind in the two-site fine-scale model is -1.15, which means for every 1 SD increase in distance from hunting blind on a non-hunting day geese were 0.3 times as likely to choose that location ($\exp(-1.15)$) when all other predictor values were held constant. To interpret interaction effects, the interaction coefficient is added to the main effect coefficients of both interaction terms. For example, the log relative selection strength for developed land on a hunting day in the two-site fine-scale model is -8.64, which is the estimated coefficient for developed land on a hunting day (the interaction term, $\beta = -0.92$) plus the estimated coefficient of the main effect of developed land ($\beta = -7.41$) and the estimated coefficient of the main effect of hunting day ($\beta = -0.31$). The relative selection of developed land on a hunting day was 0.0001 ($\exp(-8.64)$), whereas the relative selection of developed land on a non-hunting day was 0.0006 ($\exp(-7.41)$). In both circumstances a goose was less likely to choose developed land than open water because the relative selection strength was less than 1.

Resource Selection During Hunting

Coarse Scale

At the coarse scale of analysis, we estimated the log relative selection of the WMA during non-hunting periods to be 5.14, meaning geese were 170 times ($\exp(5.14)$) more likely to select for being on the WMA than off the WMA outside the hunting periods. Similarly, we estimated the log relative selection of the WMA during non-hunting days to be 5.13. The estimated log relative selection for the WMA during hunting periods was 5.12, which is the main effect of being on the WMA ($\beta = 5.14$) plus the main effect of hunting periods ($\beta = -0.03$) and the additional effect of being on the WMA during a hunting period ($\beta = 0.01$). Notably, the main effect of hunting period and the interaction effect of the WMA during a hunting period had 98% confidence intervals that overlapped zero, meaning hunting period had a negligible effect on a goose selecting the WMA. Although the confidence intervals overlapped zero, we saw that relative selection for being on the WMA was lower during hunting periods ($\exp(5.12) = 167$) than non-hunting periods ($\exp(5.14) = 170$), but in both circumstances geese were more likely to choose to be on the WMA than off the WMA because the log relative selection strengths were greater than zero. The estimated log relative selection for the WMA during hunting days was 5.14, which is the main effect of being on the WMA ($\beta = 5.13$) plus the main effect of hunting days ($\beta = -0.06$) and the additional effect of being on the WMA during a hunting day ($\beta = 0.07$). Relative selection for the WMA was slightly higher during hunting days ($\exp(5.14) = 170$) than non-hunting days ($\exp(5.13) = 169$), but in both circumstances geese were more likely to choose to be on the WMA than off the WMA because the relative selection strengths were greater than 1. Estimated coefficients (i.e., log relative selection strengths) and their 98% confidence intervals are provided in Table 1-5.

Table 1-5: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for coarse-scale resource selection functions.

Parameter	Coefficient	98% CI
Main Effects		
On WMA (hunting day model)	5.13	5.10 – 5.16
On WMA (hunting period model)	5.14	5.10 – 5.18
Hunt Day	-0.06	-0.12 – -0.01
Hunt Period ^	-0.03	-0.08 – 0.02
Interactions		
On WMA x Hunt Day	0.07	0.01 – 0.13
On WMA x Hunt Period ^	0.01	-0.04 – 0.06
^ Parameter's 98% confidence interval overlaps zero. Reference category is off-WMA outside the hunting day/period.		

Two-Site Fine Scale

Using the two-site fine-scale model, we estimated the log relative selection of grassland on non-hunting days to be -3.82 when the distance from water, precipitation, and temperature were all at their average values for the study period (zero on the standardized scale), meaning geese were 45 times ($\exp(|-3.82|)$) more likely to select open water than grassland. The estimated log relative selection for grassland on hunting days was -4.26, which is the main effect of grassland ($\beta = -3.82$) plus the main effect of hunting days ($\beta = -0.31$) and the additional effect of being in grassland on a hunting day ($\beta = -0.13$). Relative selection for grassland was lower during hunting days ($\exp(-4.26) = 0.01$) than non-hunting days ($\exp(-3.82) = 0.02$), meaning hunting decreased the likelihood of a goose choosing grassland over open water. However, in both circumstances a goose was less likely to choose grassland than open water because the relative selection strength was less than 1. The estimated log relative selection of cropland on non-hunting days when the distance from water, precipitation, and temperature were all at their average values for the study period was -3.57, meaning geese were 35 times ($\exp(|-3.57|)$) more likely to select open water than cropland. The estimated log relative selection for cropland on hunting days was -4.41, which is the main effect of cropland ($\beta = -3.57$) plus the main effect of hunting days ($\beta = -0.31$) and the additional effect of being in

cropland on a hunting day ($\beta = -0.53$). Relative selection for cropland was lower during hunting days ($(\exp(-4.41) = 0.01)$) than non-hunting days ($(\exp(-3.57) = 0.02)$), meaning hunting decreased the likelihood of a goose choosing cropland over open water. However, in both circumstances a goose was less likely to choose cropland than open water because the relative selection strength was less than 1. These results match our prediction that relative selection of grassland and cropland, where most hunting originates, would decrease on hunting days. We also predicted that selection for open water would increase on hunting days because few blinds were located near water and the geese would use it as a refuge. However, the estimated log relative selection of open water on hunting days was -0.31 , meaning geese were less likely to choose open water on a hunting day relative to a non-hunting day because the value was less than zero. Interpreting the relative selection of open water on hunting days does not involve summing additional effects because the main effect of open water is the intercept term, and the main effect of hunting day uses open water as the reference category.

The estimated log relative selection of distance from hunting blind on non-hunting days when the distance from water, precipitation, and temperature were all at their average values for the study period (i.e., zero on the standardized scale) was -1.15 , meaning geese were 0.3 times ($\exp(-1.15)$) as likely to choose an area with each 1 SD increase in distance from a hunting blind on a non-hunting day (i.e., geese preferred areas closer to blinds). The estimated log relative selection of distance from hunting blind on hunting days was -1.60 , which is the main effect of distance from blind ($\beta = -1.15$) plus the main effect of hunting days ($\beta = -0.31$) and the additional effect of distance from blind on a hunting day ($\beta = -0.14$). On a hunting day, geese were 0.2 times ($\exp(-1.60)$) as likely to choose an area with each 1 SD increase in distance from a hunting blind (i.e., geese preferred areas closer to blinds). On both hunting and non-hunting days, geese preferred to be closer to blinds, and the preference was stronger on hunting days. This was the opposite relationship than we predicted. The estimated log relative selection of distance from hunting blind with an increasing number of hunters on the landscape was -0.91 , which is the main effect of distance from blind ($\beta = -1.15$) plus the main effect of number of hunters ($\beta = 0.11$) and the additional effect of distance from blind as the number of hunters increased ($\beta = 0.13$). With each 1 SD unit increase in distance from hunting blind given a certain

number of hunters, a goose was 0.4 times ($\exp(-0.91)$) as likely to choose that area. Geese increasingly preferred to be farther from blinds as the number of hunters increased.

Notably, geese preferred open water over all other habitat types ($\beta_{\text{grass}} = -3.82$, $\beta_{\text{crop}} = -4.07$, $\beta_{\text{forest}} = -3.51$, $\beta_{\text{developed}} = -7.41$), and the largest effect sizes in this model were habitat modified by distance from water ($(\beta_{\text{grass}*\text{distWater}} = -4.58$, $\beta_{\text{crop}*\text{distWater}} = -3.57$, $\beta_{\text{forest}*\text{distWater}} = -2.99$, $\beta_{\text{developed}*\text{distWater}} = -5.87$). Estimated coefficients (i.e., log relative selection strengths) and their 98% confidence intervals are provided in Table 1-6 and Figure 1-2.

Table 1-6: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for hunting season fine-scale resource selection functions fit to both sites and only Middle Creek WMA.

Parameters are grouped by interaction terms, which are indicated with an ‘x’ at the end of the group header. The exception is the first group, which is comprised of the main effects of each habitat type. ‘Reference’ parameters represent the main effect of the group’s title term. The reference habitat category is open water.

Parameter	Two-Site		Middle Creek	
	Coefficient	98% CI	Coefficient	98% CI
Habitat				
Grassland	-3.82	-3.87 – -3.78	--	--
Cool Grass	--	--	-4.82	-4.99 – -4.65
Warm Grass	--	--	-17.59	-18.20 – -16.99
Cropland	-4.07	-4.15 – -3.99	--	--
Corn	--	--	-6.30	-6.67 – -5.94
Wheat	--	--	-8.57	-9.24 – -7.91
Hay	--	--	-7.34	-8.39 – -6.29
Forest	-3.51	-3.55 – -3.47	-23.52	-24.14 – -22.91
Developed	-7.41	-8.28 – -6.55	-30.44	-40.81 – -20.07
Distance from Water* x				
Grassland	-4.58	-4.64 – -4.52	--	--
Cool Grass	--	--	-4.08	-4.26 – -3.89
Warm Grass	--	--	-15.48	-16.05 – -14.91
Cropland	-3.57	-3.70 – -3.43	--	--
Corn	--	--	-3.89	-4.35 – -3.43
Wheat	--	--	-6.50	-7.28 – -5.72
Hay	--	--	-3.63	-5.06 – -2.20
Forest	-2.99	-3.05 – -2.94	-21.13	-21.70 – -20.56
Developed	-5.87	-6.93 – -4.81	-25.98	-35.44 – -16.53

Parameter	Two-Site		Middle Creek	
	Coefficient	98% CI	Coefficient	98% CI
Hunt Day x				
Reference	-0.31	-0.38 – -0.21	-4.18	-4.56 – -3.80
Distance from Water	-0.22	-0.29 – -0.16	-1.10	-1.41 – -0.79
Grassland	-0.13	-0.16 – -0.11	--	--
Cool Grass	--	--	0.26	0.17 – 0.34
Warm Grass	--	--	0.41	0.32 – 0.50
Cropland	-0.53	-0.62 – -0.43	--	--
Corn	--	--	-1.61	-2.01 – -1.21
Wheat	--	--	-1.20	-1.72 – -0.69
Hay ^	--	--	-0.57	-1.39 – 0.25
Forest ^	0.05	0.02 – 0.09	0.05	-0.01 – 0.11
Developed ^	-0.92	-1.37 – -0.48	-0.47	-1.06 – 0.13
Distance from Hunting Blind x				
Reference	-1.15	-1.17 – -1.12	1.12	1.00 – 1.23
Hunt Day	-0.14	-0.19 – -0.10	-4.42	-4.62 – -4.22
Number of Hunters x				
Reference	0.11	0.09 – 0.12	5.77	5.52 – 6.02
Distance from Blind	0.13	0.11 – 0.15	7.80	7.49 – 8.10
Daily Precipitation x				
Reference	0.05	0.04 – 0.06	0.08	0.06 – 0.09
Grassland	-0.08	-0.09 – -0.06	--	--
Cool Grass	--	--	-0.32	-0.36 – -0.29
Warm Grass	--	--	-0.52	-0.59 – -0.45
Cropland	0.20	0.17 – 0.23	--	--
Corn	--	--	0.33	0.26 – 0.40
Wheat	--	--	0.43	0.34 – 0.52
Hay	--	--	0.25	0.04 – 0.47
Forest	-0.15	-0.16 – -0.13	-0.12	-0.14 – -0.09
Developed ^	-0.05	-0.25 – 0.14	-0.30	-0.66 – 0.05
Daily Low Temperature x				
Reference	-0.32	-0.33 – -0.32	-0.13	-0.14 – -0.11
Grassland	0.68	0.66 – 0.69	--	--
Cool Grass	--	--	0.44	0.41 – 0.48
Warm Grass ^	--	--	0.03	-0.01 – 0.07
Cropland	0.35	0.31 – 0.40	--	--
Corn	--	--	0.27	0.18 – 0.36
Wheat ^	--	--	0.01	-0.11 – 0.14

Parameter	Two-Site		Middle Creek	
	Coefficient	98% CI	Coefficient	98% CI
Hay	--	--	0.68	0.35 – 1.01
Forest	0.85	0.83 – 0.86	0.48	0.45 – 0.51
Developed	1.15	0.91 – 1.39	1.24	0.88 – 1.60

^ Parameter's 98% confidence interval overlaps zero.
 * The main effect of distance from water was excluded because it is confounded with the open water habitat type.

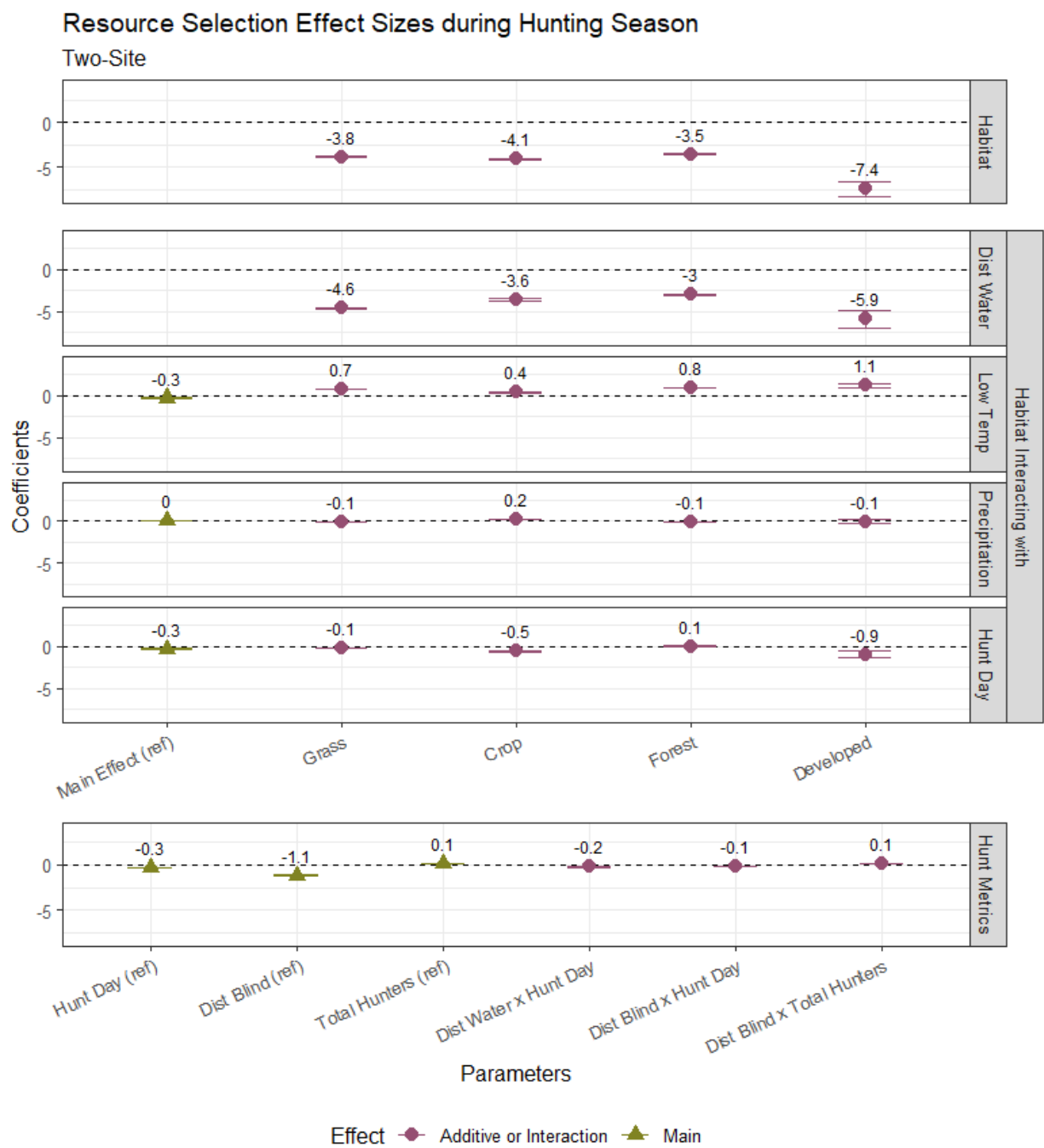


Figure 1-2: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for hunting season two-site fine-scale resource selection function. Parameters described as ‘(ref)’ are the main effect of that term. The reference habitat category is open water. The main effect of distance from water was excluded because it is confounded with the open water habitat type.

Middle Creek Fine Scale

Using the Middle Creek fine-scale model, we estimated the log relative selection of cool grasses on non-hunting days to be -4.82 when the distance from water, precipitation, and temperature were all at their average values for the study period (zero on the standardized scale), meaning geese were 124 times ($\exp(|-4.82|)$) more likely to select open water than cool grasses. The estimated log relative selection for cool grasses on hunting days was -8.74, which is the main effect of cool grasses ($\beta = -4.82$) plus the main effect of hunting days ($\beta = -4.18$) and the additional effect of being in cool grasses on a hunting day ($\beta = 0.26$). Relative selection for cool grasses was lower during hunting days ($(\exp(-8.74) = 0.0001)$) than non-hunting days ($(\exp(-4.82) = 0.008)$), meaning hunting decreased the likelihood of a goose choosing cool grasses over open water. However, in both circumstances a goose was less likely to choose cool grasses than open water because the relative selection strength was less than 1. The estimated log relative selection of corn on non-hunting days when the distance from water, precipitation, and temperature were all at their average values for the study period was -6.30, meaning geese were 544 times ($\exp(|-6.30|)$) more likely to select open water than corn. The estimated log relative selection for corn on hunting days was -12.09, which is the main effect of corn ($\beta = -6.30$) plus the main effect of hunting days ($\beta = -4.18$) and the additional effect of being in corn on a hunting day ($\beta = -1.61$). Relative selection for corn was lower during hunting days ($(\exp(-12.09) = 0.000005)$) than non-hunting days ($(\exp(-6.30) = 0.001)$), meaning hunting decreased the likelihood of a goose choosing corn over open water. However, in both circumstances a goose was less likely to choose corn than open water because the relative selection strength was less than 1. These results matched our prediction that relative selection of cool grasses and corn, where most hunting originates, would decrease on hunting days. We also predicted that relative effect of hunting day in cool grasses and corn habitats would be more strongly negative than in wheat and hay habitats, which was not supported by the results. The relative effect of hunting day in cool grasses was -4.55, which is the main effect of hunting day ($\beta = -4.18$) plus the effect of being in cool grasses on a hunting day ($\beta = 0.26$). The relative effect of hunting day in corn was -5.79, which is the main effect of hunting day ($\beta = -4.18$) plus the effect of being in corn on a hunting day ($\beta = -1.61$). The relative effect of hunting day in wheat was -5.38, which is the

main effect of hunting day ($\beta = -4.18$) plus the effect of being in wheat on a hunting day ($\beta = -1.20$). Although the confidence interval overlapped zero, we found that the relative effect of hunting day in hay was -4.75 , which is the main effect of hunting day ($\beta = -4.18$) plus the effect of being in hay on a hunting day ($\beta = -0.57$).

The estimated log relative selection of distance from hunting blind was 1.12 on non-hunting days when the distance from water, precipitation, and temperature were all at their average values for the study period, meaning geese were 3 times ($\exp(1.12)$) as likely to choose an area with each 1 SD increase in distance from a hunting blind on a non-hunting day (i.e., geese preferred areas farther from blinds). The estimated log relative selection of distance from hunting blind on hunting days was -7.48 , which is the main effect of distance from blind ($\beta = 1.12$) plus the main effect of hunting day ($\beta = -4.18$) and the additional effect of distance from blind on a hunting day ($\beta = -4.42$). On a hunting day, geese were 0.0005 times ($\exp(-7.48)$) as likely to choose an area with each 1 SD increase in distance from a hunting blind (i.e., geese preferred areas closer to blinds). On non-hunting days geese preferred to be farther from blinds, but on hunting days geese preferred to be closer to blinds. This was the opposite relationship than we predicted.

The estimated log relative selection of distance from hunting blind with an increasing number of hunters at the two nearest blinds was 14.69 , which is the main effect of distance from blind ($\beta = 1.12$) plus the main effect of number of hunters ($\beta = 5.77$) and the additional effect of distance from blind as the number of harvest attempts increased ($\beta = 7.80$). With each 1 SD unit increase in distance from hunting blind given a certain number of hunters, a goose was 2.3 million times ($\exp(14.69)$) as likely to choose that area. Geese strongly and increasingly preferred to be farther from blinds as the number of hunters increased, which matched our prediction.

Notably, like the two-site model, geese preferred open water over all other habitat types ($\beta_{\text{grassCool}} = -4.82$, $\beta_{\text{grassWarm}} = -17.59$, $\beta_{\text{corn}} = -6.30$, $\beta_{\text{wheat}} = -8.57$, $\beta_{\text{hay}} = -7.34$, $\beta_{\text{forest}} = -23.52$, $\beta_{\text{developed}} = -30.44$). Unlike the two-site model, the effect sizes of hunting were as large as the effect sizes of habitat modified by distance from water. Estimated coefficients (i.e., log relative

selection strengths) and their 98% confidence intervals are provided in Table 1-6 and Figure 1-3.

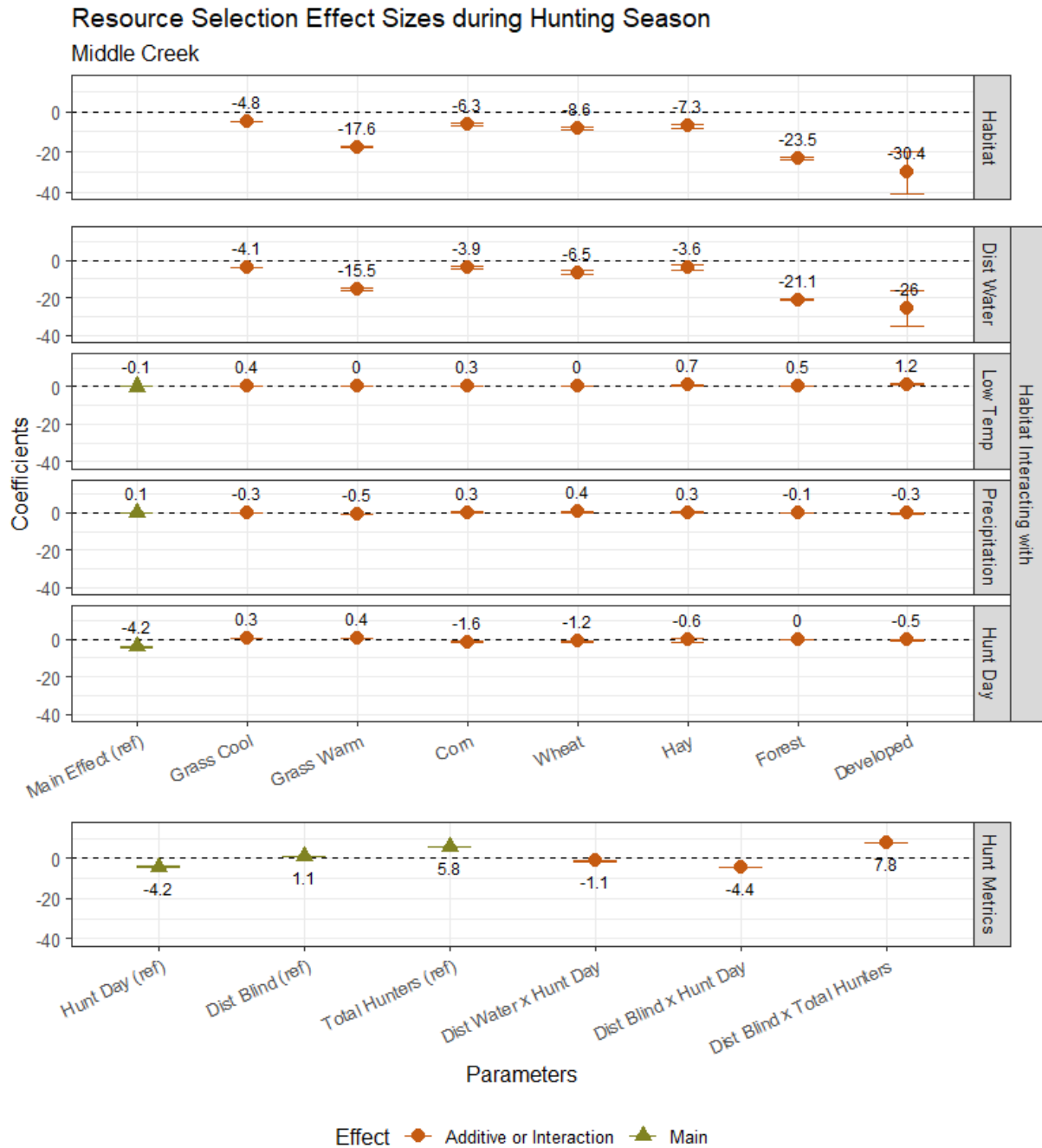


Figure 1-3: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for Middle Creek hunting season resource selection function. Parameters described as ‘(ref)’ are the main effect of that term. The reference habitat category is open water. The main effect of distance from water was excluded because it is confounded with the open water habitat type

Home Range Estimation

Home range size and overlap at each WMA and each time scale is provided in Table 1-7. The average ratio of home range size during hunting period to non-hunting period was 1.23, but sizes were not significantly different ($p=0.1$). The average ratio of home range size during hunting day to non-hunting day was 0.95, and sizes were not significantly different ($p=0.07$). The effect size of hunting was -0.18 at the fine scale (hunting day) and -0.07 at the coarse scale (hunting period). When compared separately, the average home range sizes during hunting and non-hunting days at Middle Creek were not significantly different ($p=0.6$), but they were significantly different at Pymatuning ($p<0.00001$). The average percent of non-hunting period home range that was also used during the hunting period was 63.7, whereas the average percent of non-hunting day home range that was also used during hunting days was 72.5. The average proportion of observations on the WMA during the hunting period was 0.88 compared to 0.88 during the non-hunting period. The average percent of observations on the WMA during hunting days was 0.89 compared to 0.88 during non-hunting days.

Table 1-7: Summary of home range size and location changes in relation to hunting.

Time Scale	Summary Statistics	Pymatuning WMA		Middle Creek WMA		Combined WMAs	
		Average	Range	Average	Range	Average	Range
Coarse	Hunting Period Area (km ²)	11.1	3.2 – 47.9	15.6	0.7 – 165.6	12.9	0.7 – 165.6
	Non-hunting Period Area (km ²)	10.7	3.3 – 38.7	12.5	2.4 – 147.6	11.5	2.4 – 147.6
	Ratio of Hunting to Non-hunting Area	1.20	0.37 – 4.22	1.26	0.21 – 8.58	1.23	0.21 – 8.56
	% Overlap of Non-hunting Area by Hunting Area	65.2	29.5 – 100	61.8	20.5 – 100	63.7	20.5 - 100
Fine	Hunting Day Area (km ²)	13.7	1.8 – 136.4	17.65	0.7 – 179.0	15.3	0.7 – 179.0
	Non-hunting Day Area (km ²)	15.7	0.3 – 134.3	18.6	0.5 – 179.5	17.0	0.5 – 179.5
	Ratio of Hunting to Non-hunting Area	0.85	0.46 – 1.53	1.07	0.04 – 3.45	0.95	0.04 – 3.45
	% Overlap of Non-hunting Area by Hunting Area	74.7	35.8 – 98.3	69.4	4.4 – 100	72.5	4.4 - 100

Resource Selection During Breeding Season

Two-Site

During the nesting phase geese selected most strongly for cropland ($\beta = 1.43$) followed by grassland ($\beta = 1.16$), and avoided developed land relative to open water ($\beta = -0.79$). During the gosling phase, geese selected most strongly for cropland ($\beta = 1.00$) followed by grassland ($\beta = 0.43$) and developed land ($\beta = 0.03$). During the fledged phase, geese selected most strongly for open water (reference category) followed by cropland ($\beta = -0.43$) and grassland ($\beta = -0.63$), which have negative selection strengths because open water was the most strongly preferred habitat type. These log relative selection strengths did not match our predictions. Cropland was preferred more strongly than we expected for this time of year, and developed land was mostly avoided relative to the other habitat types. The log relative selection of distance from water was -1.92 during the nesting phase and -1.76 during the gosling phase, meaning geese were 0.1 times ($\exp(-1.92)$) as likely to choose an area with each 1 SD increase in distance from water during the nesting phase and 0.1 times ($\exp(-1.76)$) as likely during the gosling phase (i.e., geese preferred areas closer to water). However, during the fledged phase, the log relative selection of distance from water was -0.31 , meaning geese were 0.7 times ($\exp(-0.31)$) as likely to choose an area with each 1 SD increase in distance from water. During all phases geese preferred to be closer to water, but the relative preference was much stronger during the nesting and gosling phases than the fledged phase. Estimated coefficients (i.e., log relative selection strengths) and their 98% confidence intervals are provided in Table 1-8 and Figure 1-4.

Table 1-8: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for breeding season resource selection functions.

Each breeding phase was fit as a separate model. The reference category is open water habitat.

Parameter	Both WMAs		Middle Creek	
	Coefficient	98% CI	Coefficient	98% CI
Nesting				
Grassland	1.16	1.11 – 1.21	--	--
Cool Grass	--	--	0.93	0.84 – 1.02
Warm Grass	--	--	1.03	0.95 – 1.11
Cropland	1.43	1.36 – 1.50	--	--
Corn	--	--	0.88	0.76 – 0.99
Wheat	--	--	1.34	1.22 – 1.47
Hay	--	--	1.01	0.82 – 1.19
Forest ^	0.27	0.21 – 0.33	0.07	-0.01 – 0.16
Developed	-0.79	-1.11 – -0.46	-0.86	-1.40 – -0.32
Distance from Water	-1.92	-1.98 – -1.87	-3.39	-3.51 – -3.27
Gosling				
Grassland	0.43	0.38 – 0.48	--	--
Cool Grass	--	--	0.91	0.83 – 0.99
Warm Grass	--	--	-1.17	-1.31 – -1.04
Cropland	1.00	0.94 – 1.07	--	--
Corn	--	--	1.26	1.17 – 1.36
Wheat	--	--	1.82	1.72 – 1.92
Hay	--	--	0.62	0.44 – 0.80
Forest	-1.06	-1.12 – -0.99	-1.08	-1.18 – -0.98
Developed ^	0.03	-0.15 – 0.20	-0.79	-1.22 – -0.35
Distance from Water	-1.76	-1.82 – -1.70	-3.08	-3.21 – -2.96
Fledged				
Grassland	-0.63	-0.67 – -0.59	--	--
Cool Grass	--	--	-1.28	-1.38 – -1.18
Warm Grass	--	--	-2.59	-2.73 – -2.45
Cropland	-0.45	-0.50 – -0.40	--	--
Corn	--	--	-0.96	-1.07 – -0.85
Wheat	--	--	0.93	0.85 – 1.01
Hay	--	--	-0.16	-0.29 – -0.02
Forest	-4.12	-4.22 – -4.03	-2.39	-2.48 – -2.29
Developed	-1.74	-1.92 – -1.55	-1.88	-2.27 – -1.48

Parameter	Both WMAs		Middle Creek	
	Coefficient	98% CI	Coefficient	98% CI
Distance from Water	-0.31	-0.35 – -0.28	-2.18	-2.30 – -2.07

^ Parameter's 98% confidence interval overlaps zero.

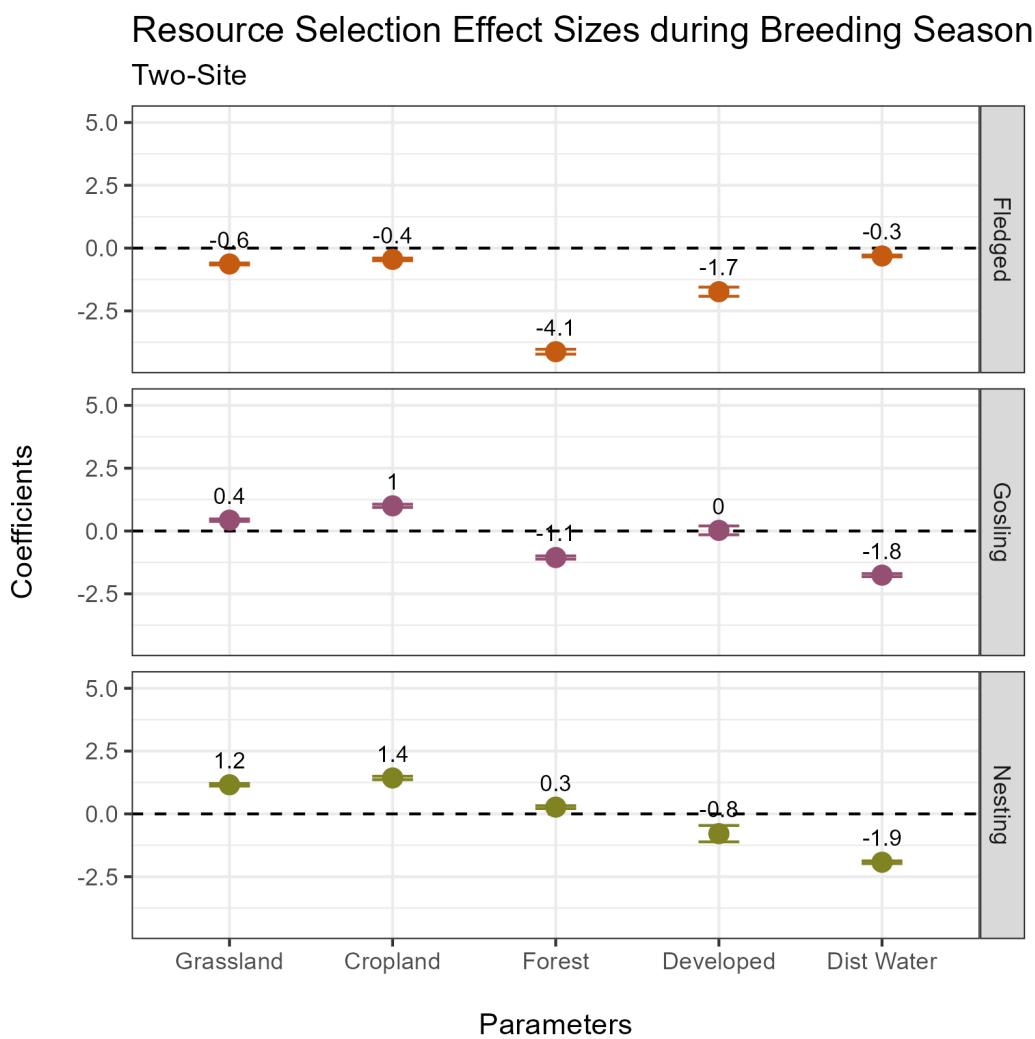


Figure 1-4: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for the breeding season two-site resource selection function. The reference category is open water.

Middle Creek

During the nesting phase geese selected most strongly for wheat ($\beta = 1.34$) followed by warm season grasses ($\beta = 1.03$), hay ($\beta = 1.01$), cool season grasses ($\beta = 0.93$), and corn ($\beta = 0.88$). During the gosling phase, geese selected most strongly for wheat ($\beta = 1.82$) and corn ($\beta = 1.26$). During the fledged phase, geese selected most strongly for wheat ($\beta = 0.93$) and open water (reference category). These log relative selection strengths did not match our predictions. During the nesting phase there was nearly equivalent selection strength across the grassland and cropland categories, and during the gosling phase there was relatively strong selection for several types of crops. The log relative selection of distance from water was -3.39 during the nesting phase, -3.08 during the gosling phase, and -2.18 during the fledged phase, meaning geese were 0.03 times ($\exp(-3.39)$) as likely to choose an area with each 1 SD increase in distance from water during the nesting phase, 0.04 times ($\exp(-3.08)$) as likely during the gosling phase, and 0.1 times ($\exp(-2.18)$) during the fledged phase. Geese preferred to be closer to water during all phases, but, unlike the two-site model, the relative preference was only slightly stronger during the nesting and gosling phases than the fledged phase. Estimated coefficients (i.e., log relative selection strengths) and their 98% confidence intervals are provided in Table 1-8 and Figure 1-5.

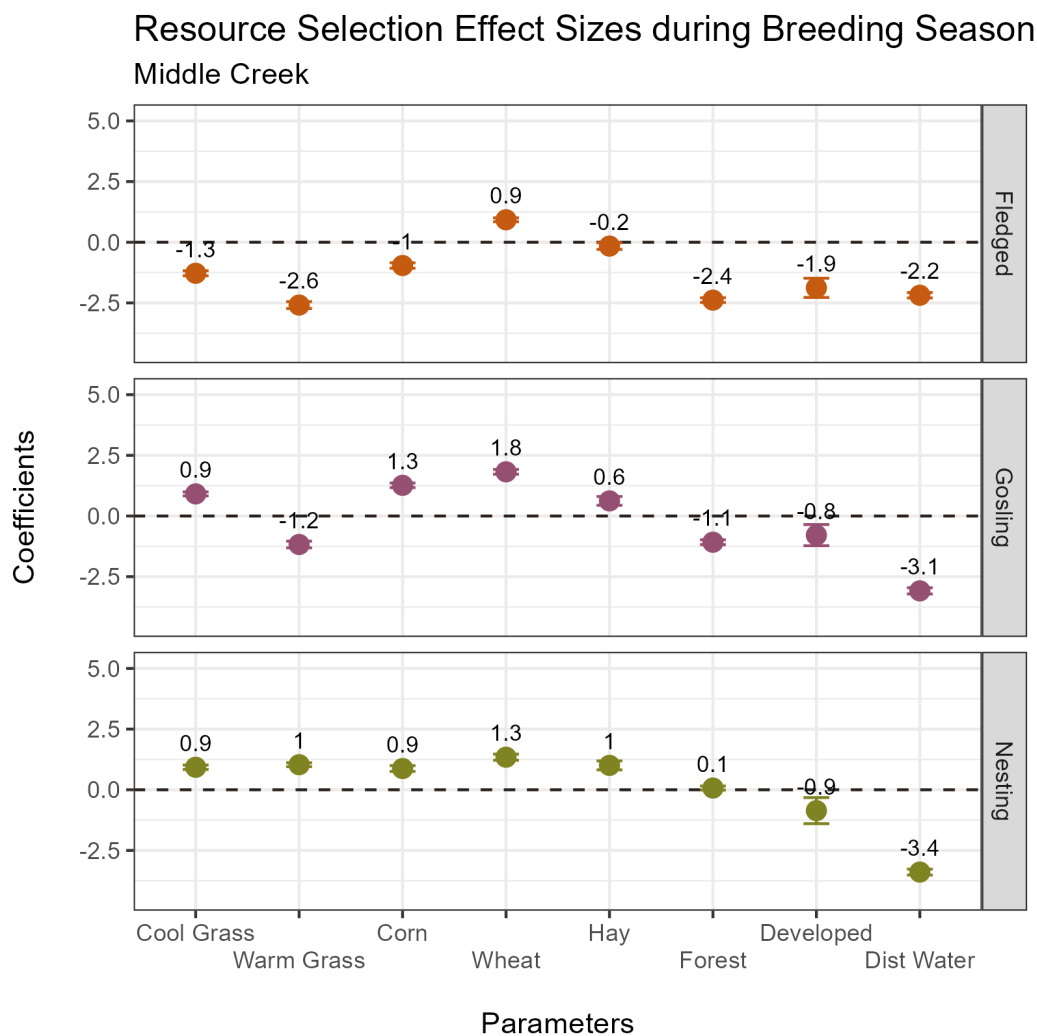


Figure 1-5: Estimated coefficients (log relative selection strength) and associated 98% confidence intervals for the breeding season Middle Creek resource selection function. The reference category is open water.

Discussion

Our study found that, among individuals who remained within seven miles of the WMAs, Canada geese did not abandon the WMAs during hunting. Whether evaluating hunting impacts on the fine temporal scale (hunting days) or coarse temporal scale (hunting periods), resident geese spent an equal proportion of time on the WMAs during hunting and non-hunting and were at least 165 times more likely to choose to be on the WMA than off the WMA. This finding

partially contradicts our hypothesis and findings from similar waterfowl studies, where individuals employed short-term abandonment to avoid predation but maintained long-term site fidelity (Bregnballe & Madsen, 2004; Dooley et al., 2010; Roy et al., 2013). Our results expand on this prior research by specifying that, if individuals find sufficient refuge within a hunted area, they will not abandon the site even temporarily. This conclusion is further supported by our findings that a) individuals spent an equivalent amount of time on the WMAs during non-hunting and hunting, and b) individual home ranges only partially overlapped between non-hunting and hunting, meaning geese shifted their home ranges within the WMA boundaries during hunting presumably to seek refuge without leaving the sites. This indicates that geese found sufficient resources on the WMAs to encourage fidelity, including both spatial refuge from predation threat and food (Lima & Bednekoff, 1999; Magle et al., 2014; Roy et al., 2013). Notably, the strong site fidelity in our results may be due to the focused capture efforts of resident populations on each WMA. However, the PGC is actively targeting these goose populations in their management efforts and the implications of any population-specific behavioral characteristics are relevant to management objectives.

Both Pymatuning and Middle Creek have lakes where hunting pressure is low to nonexistent, and those areas may have provided a refuge from hunting pressure. Geese showed a clear preference for open water relative to the other land cover types in both fine-scale models. Relative selection for open water was at least 33 times greater than all other habitat types. Further, the largest magnitude effect sizes in the two-site model were the interactions of distance from water with habitat type, meaning the effect of being near water was stronger than any hunting-related effect. However, in the Middle Creek analysis, the effect sizes of the hunting metrics were equivalent or larger than the distance from water interaction effects. At Middle Creek, 8 blinds were located within 25 meters of open water (all near small, scattered ponds and none near the large central lake), but at Pymatuning no blinds were located close to water. Thus, open water habitats may have served as spatial refuge during hunting while also meeting basic resource needs. The fact that one third of the hunting blinds at Middle Creek were located near water may have contributed to the stronger effects of hunting in that analysis than in the two-site analysis. Hunting activity would have impacted relatively more of the open water areas at Middle Creek, thus dulling the safety of open water and adjacent habitats.

In both fine-scale models, we found that goose preference of the habitats relative to each other were mostly unchanged between hunting and non-hunting days, meaning relative selection of habitats where hunting blinds were located was not different than habitats where hunting blinds were not located. Because the predation threat in this study was spatially and temporally predictable, it is possible that the geese maintained both a landscape of fear that allowed them to identify areas within each appealing habitat type that were far enough from a hunting blind to be a lesser threat and a schedule of fear that allowed them to choose those low-threat areas on hunting days (Laundre et al., 2010; Palmer et al., 2022). Additionally, as the number of hunters increased, geese increasingly preferred to be farther from a blind, indicating that geese perceived the magnitude of human activity on the landscape and adjusted their distance from hunting blinds accordingly.

We originally hypothesized that geese would partition their habitat selection spatially or temporally to avoid predation, which would result in a shift in home range locations during hunting periods or different habitat selection on hunting days, and we found evidence of both (Bechet et al., 2004; McGrath et al., 2018): Home ranges overlapped by only 63.7 percent when comparing hunting to non-hunting periods, and relative selection for all habitat types decreased on hunting days. Because the predation threat was spatially and temporally predictable, geese were able to minimize their threat of predation by shifting their home ranges during hunting and selecting areas that provided spatial refuge. While we were not able to experimentally test the theory of spatial refuge by changing the locations of hunting blinds, it's likely that removing the spatial or temporal predictability of the predation threat could reduce the existing refuge effect and cause geese to employ a different risk allocation method (Cleveland et al., 2012).

Our study found that geese preferred herbaceous terrestrial habitats (i.e., grassland and cropland) over open water during the nesting and gosling phases. Notably, when analyzing our data using more detailed land cover, we found that geese preferred each type of grassland and crop during the nesting phase. This preference held during the gosling phase, except for warm season grasses, which indicates that geese require heterogeneous herbaceous landscapes during the breeding season and suggests that monocultures may not provide sufficient resources.

While geese did not select for open water habitat as strongly during the nesting and gosling phases compared to the fledged phase, both models indicated that geese preferred to at least be nearer to water during those phases relative to the fledged phase. The effect size of

distance from water was the strongest among all predictors, indicating that preferred habitat types (i.e., grasslands and croplands) located adjacent to water are desirable landscape features during breeding. Overall, we found that a variety of grass mixtures and cultivated crops are necessary to support the full breeding cycle of geese, including consistent access to water. To retain a resident goose population at a site year-round requires the inclusion of vegetation that is not preferred during the hunting season, such as warm season grasses.

Our study found that geese maintained both a landscape of fear and a schedule of fear, which they navigated via spatial and temporal partitioning to balance trade-offs between preferred resources and predation threats (Laundré et al., 2001; Palmer et al., 2022). Overall, our results suggest that predictable predation threats may not disrupt site fidelity in a prey species if the home site contains sufficient and consistent spatial refuge. For land managers and biologists maintaining a goose population year-round, our findings show that a heterogeneous landscape of grasslands and croplands with plentiful and proximate water sources is most desirable for geese. Conversely, for land managers wishing to deter geese from an area, eliminating waterbodies and planting swaths of tall grasses may be effective.

Chapter 2

Canada Goose Movement in Response to Hunting

Introduction

Anthropogenic activity can modify how wildlife perceive risks and rewards across the landscape and affect animal movement and behavior (Bechet et al., 2004). For prey species, predation avoidance exerts a strong influence on space-use and behavior via the landscape of fear (Laundré et al., 2001). Humans contribute to the landscape of fear by causing both direct effects (mortality) and indirect effects, such as harassment that prompts behavioral changes. Across the globe, human activity such as vehicle use, land conversion, and recreation is causing a wide range of mammal species to shift toward nocturnality (Gaynor et al., 2018). Higher levels of recreation have been shown to displace mammal activity spatially and temporally (George & Crooks, 2006; Salvatori et al., 2023). Further, a review of studies globally found that terrestrial and aquatic animals have increased their movement on average 70%, with the strongest impacts caused by human activity followed by habitat modification (Doherty et al., 2021). On a smaller scale, researchers found that, when disturbed by non-lethal human activity (e.g., jogging, mowing), birds at a wildlife refuge consistently flushed. How far an individual flushed and how long it stayed away varied by species: gulls and terns returned to their original location when the disturbance ended, ducks flushed within the vicinity of their original location, and shorebirds vacated the area entirely (Burger, 1981). This and similar studies have found that birds were less active in suitable habitats when recreation activities were higher (Burger, 1981; Rösner et al., 2014). However, a recent study testing the efficacy of harassment to deter Canada geese (*Branta canadensis*) from using certain sites found that the effect was relatively small compared to weather conditions (Askren et al., 2022), indicating that geese recognized harassment as non-lethal and responded accordingly. Similarly, ungulates in Africa displayed shorter flight initiation distances for humans that approached in hunting-free areas than hunted areas,

indicating that they distinguished a potentially non-lethal threat from a potentially lethal threat (Tarakini et al., 2014).

When perceiving a potential threat, animals might recognize it as benign and modify their behavior minimally or not at all, recognize it as lethal and attempt to avoid it, or misidentify the cue and respond ineffectively (Smith et al., 2021). Misidentifying a lethal threat can be especially problematic for an individual. For game species, hunters are part of an animal's landscape of fear, which is an individual's cognitive map that incorporates spatial variations in predation risk across the landscape (Laundre et al., 2010). Hunting-related changes in activity have been documented in mammalian and avian species. Many studies have shown that ungulate species increased their movement rates during the hunting season (C. L. Brown et al., 2020; Cleveland et al., 2012; Picardi et al., 2019), presumably as a defense mechanism, and it's been suggested that the magnitude of response is related to variation in risk exposure (Cromsigt et al., 2013). In waterfowl, graylag geese (*Anser anser*) avoided fields where they were previously shot at (Månsson, 2017). In mallards (*Anas platyrhynchos*), one study observed a decrease in mean flight distance in response to shooting as the hunting season progressed (Dooley et al., 2010), suggesting habituation to the predation threat, whereas a separate study did not observe different average flight distances when comparing movement in hunting and non-hunting areas (Link et al., 2011). Additionally, in snow geese (*Anser caerulescens*), distance flown after disturbance has been shown to decrease with flock size (Bechet et al., 2004). During the hunting season, ducks were observed moving from day roosts to foraging areas later in the evening, and leaving foraging areas earlier in the morning, indicating that animals also retain a schedule of fear (McDuie et al., 2021; Palmer et al., 2022). Further, like many ungulate species, they exhibited higher movement rates during the hunting season than the preceding non-hunting weeks. Studying movement patterns allows researchers to infer anti-predator behaviors and their drivers, which can in turn affect survival (Frid & Dill, 2002). Anti-predator behavior can be energetically costly through increased evasive movements and decreased energy intake, which can reduce an individual's body condition, lower reproductive success, and contribute to reduced population size (Dorak et al., 2017; Frid & Dill, 2002; LeTourneux et al., 2021).

As high-resolution GPS tracking data becomes more available, studies have begun analyzing the effects of external factors, including hunting, on waterfowl movement patterns. Many studies make inferences based on movement rate or flight distance during each timestep

and fit models to those isolated metrics (McDuie et al., 2019, 2021; Xu et al., 2021). However, hidden Markov models (HMMs) are well-suited for studying animal movement behavior and provide additional insights into animal behavior compared to traditional models (Patterson et al., 2009). HMMs are a type of hierarchical model comprised of observable data and unobservable (i.e., hidden or latent) states, where the latent states represent the process of interest (Zucchini & MacDonald, 2009). In animal movement modeling, the observed states are typically a quantifiable aspect of the animal's movement, such as step length or turning angle, and the latent states are behaviors that relate to the observable states (Auger-Méthé et al., 2021; Nicosia et al., 2017). In HMMs the latent state at the current time is related to the state at the previous time. The model estimates the likelihood that an individual is expressing a certain latent state at each timestep based on the observed step lengths and turning angles. The transition probabilities between latent states can also be modeled as a function of predictor variables, such as individual attributes or environmental conditions, which then describe how variables affect the probability of being in each state. Based on how each predictor affects the transition probabilities, a researcher can infer the behavioral strategy an animal employs to minimize risk. For example, researchers found that female killer whales (*Orcinus orca*) were more likely to halt foraging when vessels were in close proximity (Holt et al., 2021).

Understanding anti-predator behaviors and what prompts them can improve population management by allowing biologists to minimize perceived threats and help preserve individuals' energy expenditures. The Pennsylvania Game Commission (PGC) operates several Wildlife Management Areas (WMAs) to maximize waterfowl hunting quality by providing Canada geese with breeding and foraging habitat and spatial and temporal relief from hunting pressure. The PGC enforces modified hunting regulations on certain WMAs, such as shorter hunting seasons, lower bag limits compared to elsewhere in the commonwealth, a limited number of hunters per day, and static hunting locations (Lau & Yeager, 2021). The primary goal of this study was to understand how predation in the form of hunting affects prey movement. Understanding how game species' movement changes in response to hunting can guide management decisions to maximize species abundance and hunting opportunities as well as elucidate behavioral adaptations to predation threat. We fit hidden Markov models using fine-scale telemetry data from non-migratory Canada geese to determine how goose movement patterns varied with hunting pressure.

Methods

Details regarding the study area, field methods, and animal tracking can be found in the Methods section of Chapter 1.

Data Processing

Data were downloaded from Movebank (Kays et al., 2022) and processed using R (R Core Team, 2022). Locations were collected in both the World Geodetic System 1984 (WGS84) and Universal Transverse Mercator (UTM) coordinate reference systems, and we used UTM Zone 17 and 18 location data for Pymatuning and Middle Creek WMA, respectively. Locations with a horizontal dilution of precision value greater than 2.0 were removed from the sample due to presumed low accuracy (Specht, 2022). For each bird, location records with duplicated timestamps were removed (n=900), and the duplicate record containing the most metadata was retained.

Because our modeling procedure required temporally regular location data, we imputed locations for missing timestamps using the *'crawl'* package in R (D. S. Johnson et al., 2008; D. S. Johnson & London, 2018; Zucchini & MacDonald, 2009). Step lengths and turn angles were calculated for each observation using the *'momentuHMM'* package (McClintock & Michelot, 2018). Subsequently, date-time stamps were set to local time using the *'lubridate'* package to account for daylight savings time (Garrett Grolemond & Hadley Wickham, 2011), and observations were filtered to legal hunting hours at each WMA (Pymatuning: 05:00-12:30, Middle Creek: 05:00-13:30).

Hunting occurs across seasonal and daily timescales; therefore, we analyzed space-use at both coarse and fine spatial and temporal scales. For a coarse scale analysis, we limited observations to locations marked within seven miles of the boundary of each WMA during the on-WMA hunting season (i.e., hunting periods plus the mid-season non-hunting 'split' period) plus seven days before and after. We buffered the WMA by seven miles for this analysis to allow comparison between bird movement on and off the WMA. We included individuals that had at least two weeks of observations, such that the data captured at least one week of a non-hunting

period and one week of a hunting period. For a fine-scale analysis, we limited the observations to locations observed within the boundary of each WMA during the WMA-specific hunting periods plus one day before and after (Table 1-1, Figure 1-1) (D. Jones, personal communication, 14 Feb 2022). At this scale we excluded the mid-season non-hunting ‘split’ period, which is a several-week period during which hunting is not allowed on the WMAs. Excluding the non-hunting ‘split’ period allowed us to directly compare hunting and non-hunting days during the on-WMA hunting season and determine whether geese respond to hunting differently when the temporal refuge is short-lived. We included individuals that had at least four days of observations, such that the data captured at least two non-hunting days and two hunting days. We conducted two analyses at the fine scale: one used data from both WMAs (hereafter referred to as “two-site fine scale”) and the other used data from only Middle Creek (hereafter referred to as “Middle Creek fine scale”) to make use of higher resolution environmental data available exclusively for that site.

Covariates

We modeled goose movement using covariates that represented hypothesized environmental resources and risks, which are listed in Table 2-1, to estimate the latent state transition probability of geese (Matthiopoulos et al., 2015; Zucchini & MacDonald, 2009). Hunting day on-WMA was determined from the Hunter’s Digest and WMA managers (Lau & Yeager, 2021)(C. Deal, personal communication, 12 Aug 2022; L. Ferreri, personal communication, 2 Sep 2022), and hunting period on-WMA was derived from hunting days and constitutes a consecutive period of alternating hunting and non-hunting days (Table 1-1, Figure 1-1). Hunting intensity was represented by number of hunters as recorded by PGC staff during hunting check-in (C. Deal, personal communication, 28 Feb 2022 and 24 Feb 2023; S. Ferreri, personal communication, 8 Feb 2022; B. Collett, personal communication, 17 Feb 2023). We chose number of hunters to represent hunting intensity because the value was independent of goose presence near a blind. Larger values indicate more hunters on a given day and thus represent a higher hunting intensity. At Middle Creek, the records of hunting intensity were maintained on a per-blind per-day basis. Therefore, for the two-site fine-scale analysis we

aggregated the daily metrics across the entire WMA to match the resolution of the data available from Pymatuning WMA. For the Middle Creek analysis, we calculated hunting intensity for each observation by multiplying the number of hunters at each blind by the inverse distance between each blind and each observed location and averaging that value across the two nearest blinds. So, a larger value indicates that an observation is located very close to more hunters, a mid-range value could indicate that an observation is located closer to fewer hunters or farther from many hunters, and a small value indicates that an observation is located farther from relatively few hunters. The maximum number of hunters per blind was four. Habitat was delineated using the USGS National Land Cover Dataset (2019), projected from a 30-meter resolution to a 10-meter resolution, and aggregated into five functional habitat categories: open water, grass, crop, forest, and developed (Jon Dewitz & U.S. Geological Survey, 2021). Distance from hunting blind was calculated at a 10-meter resolution derived from blind point locations provided by WMA managers (C. Deal, personal communication, 4 Feb 2022; S. Ferreri, personal communication, 8 Feb 2022; L. Ferreri, personal communication, 5 Sep 2022). Vegetative cover at Middle Creek was delineated and provided by the WMA managers as a shapefile with the following categories: row crop (corn, wheat, or rotational hay), warm season grass, cool season grass, old field reverting (equivalent to warm season grass), food plot (equivalent to cool season grass), or hedgerow (equivalent to forest) (S. Ferreri, personal communication, 19 Oct 2022). We used these primary categories to delineate vegetative cover, but we used the row crop subcategories to delineate the crops by type. The verified vegetative cover data were only used in a site-specific movement model for Middle Creek because Pymatuning did not have ground-truthed land cover data at a comparable resolution. The Middle Creek fine-scale model substituted the verified vegetation cover data for the NLCD data where possible because the ground-truthed data did not cover the full WMA (the ground-truthed data did not include delineations of forested, developed, and open water areas), which resulted in a blend of habitat types from both data sources. To assign covariate values to each data point, we either extracted the spatial covariate values directly from the raster layers via the *'raster'* package in R (Hijmans, 2023) or assigned non-spatial data to an observation by matching the timestamp dates. In all three analyses, continuous variables were standardized to have a mean of zero and a standard deviation of one.

Table 2-1: Model covariates included in movement models.

Variable	Description
On WMA	Goose location is outside (0) or within (1) the boundary of a WMA
Site	Pymatuning WMA (0) or Middle Creek WMA (1)
Hunting day on-WMA	Day when Canada goose hunting is (1) or is not (0) allowed in the WMA Controlled Hunting Areas
Hunting period on-WMA	Span of days that contains alternating hunting and non-hunting days on the WMA (1) or span of non-hunting days between two hunting periods (0)
Number of Hunters [†]	Daily total number of hunters on the WMA (two-site model) or Number of hunters per blind per day averaged across the two nearest blinds to each observation and weighted by the inverse distance from each blind (Middle Creek model)
Habitat	Land cover type categorized as open water, grassland, cropland, forested, or developed
Cover	Land cover type verified by Pennsylvania Game Commission staff categorized as corn, wheat, hay, cool season grass mix (includes food plots), warm season grass mix (includes reverting fields), and hedgerow (incorporated into forest category)
Distance from hunting blind [^]	Distance (m) from nearest hunting blind
[^] Value range was standardized (scaled and centered) to have a mean of 0 and standard deviation of 1.	

Statistical Analysis

We fit hidden Markov models using the *'momentuHMM'* package in R (McClintock & Michelot, 2018). Step lengths were assumed to come from a Weibull distribution because it has a heavy tail that allows for longer steps, and turning angles were assumed to come from a von Mises distribution because it is the circular analogue to the normal distribution and allows for the equivalent of a uniform distribution if appropriate (Hooten et al., 2017; Tracey et al., 2005). We did not include a random effect to account for individual heterogeneity because existing methods for incorporating discrete-valued random effects require specifying a probability for each mixture, and it would be computationally inefficient to specify more than a dozen mixtures (McClintock & Michelot, 2021). We fit HMMs at two spatiotemporal scales and applied the steps outlined by (Pohle et al., 2017) to select the number of latent states. We first decided the minimum (n=2) and maximum (n=3) number of plausible states for each analytical scale. We chose three as the maximum number of states because a null model fit with four states did not

yield biologically distinguishable states. Then, we fit a null model to the data at each scale for each number of states. We plotted the pseudo-residuals from each model and calculated AIC to compare model fit within scales. For each scale of analysis, we ultimately chose to fit a 3-state full model. We expected one state to consist of longer step lengths and smaller turn angles, which would correspond to flight. When not flying, we expected two behaviors: resting, indicated by the shortest step lengths, and feeding, indicated by moderate step lengths. After fitting the full models, we made inference on the effect of each predictor variable on the transition probabilities (γ) between latent states.

Coarse Scale

To evaluate seasonal responses to hunting pressure at a landscape scale we estimated transition probabilities between latent states as a function of an interaction between being on the WMA and hunting period, which included main effects of being on the WMA and of hunting period. Because the on-WMA and off-WMA hunting seasons mostly align, we hypothesized that movement on the WMA would not differ from movement off the WMA. Additionally, because similar studies in mammals and waterfowl found increased movement rates during hunting seasons, we hypothesized that geese would move more during hunting periods (Cleveland et al., 2012; McDuie et al., 2021; Picardi et al., 2019). Thus, we expected to see a positive effect of hunting period on the probability of switching from a ‘resting’ or ‘feeding’ state to a ‘flying’ state.

Two-Site Fine Scale

At the finer spatiotemporal scale, we estimated transition probabilities between latent states as a function of an interaction between distance from hunting blind and hunting day, which included main effects of distance from hunting blind and of hunting day. We also included additive effects of habitat and number of hunters. Again, because similar studies in mammals and waterfowl found increased movement rates during hunting seasons, we hypothesized that geese

would move more during hunting days, especially when closer to a blind, and with more hunters on the WMAs (Cleveland et al., 2012; McDuie et al., 2021; Picardi et al., 2019). Thus, we expected to see a positive effect of number of hunters on the probability of switching from a ‘resting’ or ‘feeding’ state to a ‘flying’ state, and a positive effect of hunting day on the probability of switching from a ‘resting’ or ‘feeding’ state to a ‘flying’ state, with a decreasing effect as distance from blind increases.

Middle Creek Fine Scale

At the finer scale using only Middle Creek data, we estimated transition probabilities between latent states using the same model formula as the two-site fine-scale model with one substitution: the blended vegetation cover and NLCD data to represent habitat types. We hypothesized that geese would move more during hunting days, especially when closer to a blind, and with more hunters on the WMAs (Cleveland et al., 2012; McDuie et al., 2021; Picardi et al., 2019). Like the two-site fine-scale model, we expected to see a positive effect of number of hunters and of hunting day on the probability of switching from a ‘resting’ or ‘feeding’ state to a ‘flying’ state. Because we incorporated the number of hunters at the two nearest blinds for each observed location instead of the WMA-wide number of hunters, we expected to see a stronger effect of the number of hunters, or at least a more accurate representation of that effect than estimated in the two-site model.

Results

We collected 7.4 million observed locations from 134 geese, of which up to 453,378 locations from 81 geese were included in the final analyses (Table 2-2).

Table 2-2: Number of tracked geese and observation records collected during the study and included in analysis.

WMA	Total		Coarse Scale Analysis		Fine Scale Analysis	
	Number of Geese	Number of Observations	Number of Geese	Number of Observations	Number of Geese	Number of Observations
Pymatuning	66	4,034,155	47	284,876	46	185,480
Middle Creek	68	3,374,444	34	168,502	33	71,565
Total	134	7,408,599	81	453,378	79	257,045

An HMM uses step lengths and turn angles to estimate a transition probability matrix (Γ), which includes the estimated likelihood of an individual switching between latent states (γ). For example, the likelihood of a goose remaining in a ‘resting’ state if it was in a ‘resting’ state during the prior observation is represented by the estimated value of γ_{11} . The likelihood of a goose switching to a ‘resting’ state if it was in a ‘flying’ state during the prior observation is represented by the estimated value of γ_{31} . The behavioral interpretations of each state are determined post-hoc, based on the estimated step lengths and turning angles. The effect sizes of the predictors (β) modify these estimated transition probabilities and thus increase or decrease the likelihoods. The transition probability matrix is provided in Table 2-3. Sample plots of step length and turn angle densities are provided in Appendix A, Figures A-1 and A-2. The most probable state sequence for one sample individual is mapped in Appendix A, Figure A-3.

Table 2-3: Transition probability matrix (Γ) from hidden Markov models fit to both sites at the coarse and fine spatiotemporal scales and to only Middle Creek WMA at the fine scale.

Values (γ_{ii}) represent the likelihood of an individual switching from the state listed in the row header to the state listed in the column header.

Coarse Scale			
	Resting	Feeding	Flying
Resting	0.80	0.19	0.02
Feeding	0.07	0.85	0.07
Flying	0.02	0.27	0.71
Two-Site Fine Scale			
	Resting	Feeding	Flying
Resting	0.89	0.11	0.01
Feeding	0.09	0.84	0.07
Flying	0.03	0.20	0.77
Middle Creek Fine Scale			
	Resting	Feeding	Flying
Resting	0.82	0.16	0.02
Feeding	0.10	0.81	0.09
Flying	0.10	0.26	0.64

Coarse Scale

We fit a 3-state model where the first state was interpreted as a ‘resting’ state with step lengths from a Weibull distribution with shape (κ) 1.43 and scale (λ) 8.25 and mean turn angle (μ) of 0.04 radians (rad; concentration (ϕ) = 0.27). The second state was interpreted as a ‘feeding’ state with $\kappa = 1.43$, $\lambda = 34.95$, and $\mu = 0.12$ rad ($\phi = 0.10$). The third state was interpreted as a ‘flying’ state with $\kappa = 0.76$, $\lambda = 308.52$, and $\mu = 0.01$ rad ($\phi = 0.84$).

At the coarse scale of analysis, geese on a WMA during a non-hunting period were less likely to transition from a resting to a feeding state ($\beta = -0.31$) or from a resting to a flying state ($\beta = -0.36$) than when off the WMA. Additionally, being on a WMA increased the probability of transitioning from a flying to a resting state ($\beta = 0.90$). There was no effect of hunting period on the probability of switching to a flying state when a bird was not on a WMA ($\beta_{13} = 0$, $\beta_{23} = 0$). When a bird was on a WMA during a hunting period the probability of switching from a resting

state to a flying state decreased ($\beta = -0.47 = \beta_{\text{wma}} + \beta_{\text{hunt}} + \beta_{\text{wma}*\text{hunt}} = -0.36 + 0 + -0.11$) and the probability of switching from a feeding to a flying state also decreased ($\beta = -0.23 = \beta_{\text{wma}} + \beta_{\text{hunt}} + \beta_{\text{wma}*\text{hunt}} = 0.2 + 0 + -0.43$). Our results showed that the effect of being on a WMA during a hunting period increased the likelihood of transitioning from a feeding state to a resting state ($\beta = 0.5 = \beta_{\text{wma}} + \beta_{\text{hunt}} + \beta_{\text{wma}*\text{hunt}} = 0.31 + -0.08 + 0.27$) and from a flying state to a resting state ($\beta = 1.08 = \beta_{\text{wma}} + \beta_{\text{hunt}} + \beta_{\text{wma}*\text{hunt}} = 0.9 + 0.1 + 0.08$). These findings demonstrated the opposite of what we hypothesized and indicate that geese tended to rest on the WMAs during non-hunting periods. Further, hunting increased the probability of being in a resting state and decreased the probability of taking flight. The effect sizes of each predictor on the transition probabilities are provided in Table 2-4 and depicted in Figure 2-1.

Table 2-4: Estimated coefficients (β) from hidden Markov model fit to both sites at the coarse spatiotemporal scale.

Parameters are listed as the section headers and coefficients indicate how the parameter changes the probability of transitioning from the state listed in the row header to the state listed in the column header. Estimated parameters are on the logit scale.

On WMA			
	Resting	Feeding	Flying
Resting	--	-0.31	-0.36 [^]
Feeding	0.31	--	0.20
Flying	0.90	0.05 [^]	--
Hunt Period			
	Resting	Feeding	Flying
Resting	--	-0.50	-0.00 [^]
Feeding	-0.08 [^]	--	0.00 [^]
Flying	0.10 [^]	-0.28	--
On WMA x Hunt Period			
	Resting	Feeding	Flying
Resting	--	0.14 [^]	-0.11 [^]
Feeding	0.27	--	-0.43
Flying	0.08 [^]	0.24	--

[^] Parameter's 98% confidence interval overlaps zero.

Effect of Predictors on Transition Probability

Coarse Scale Model

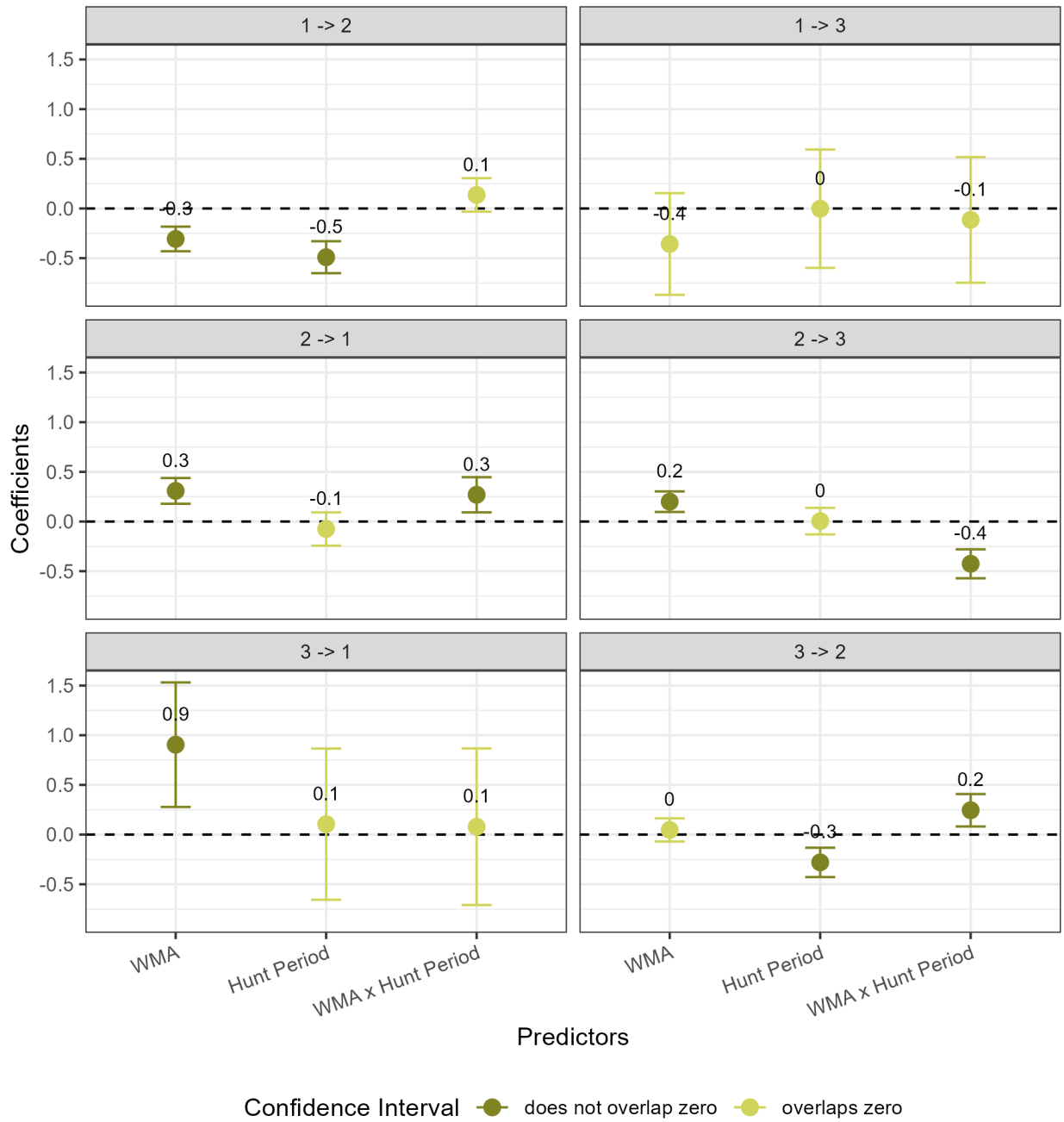


Figure 2-1: Estimated coefficients and associated 98% confidence intervals from hidden Markov model fit to both sites at the coarse spatiotemporal scale. Effect sizes are on the logit scale.

Given our hypothesis about movement behavior and our understanding of goose ecology, we interpreted state 1 as ‘resting’, state 2 as ‘feeding’, and state 3 as ‘flying.’ For example, the top left figure depicts the effect of each covariate on the probability of transitioning from resting to feeding.

Two-Site Fine Scale

At the finer spatiotemporal scale, using data from both WMAs, we fit a 3-state model where one state was interpreted as a ‘resting’ state with $\kappa = 1.43$, $\lambda = 7.47$, and $\mu = 0.05$ rad ($\phi = 0.29$), the second state was interpreted as a ‘feeding’ state with $\kappa = 1.42$, $\lambda = 31.79$, and $\mu = 0.06$ rad ($\phi = 0.14$), and the third state was interpreted as a ‘flying’ state with $\kappa = 0.77$, $\lambda = 266.50$, and $\mu = 0.02$ rad ($\phi = 0.80$).

We estimated that geese were less likely to switch from a resting to a flying state ($\beta = -0.17$) or a feeding to a flying state ($\beta = -0.41$) on a hunting day. Additionally, we estimated that on hunting days geese were more likely to transition from a feeding to a resting state ($\beta = 0.24$) and less likely to transition from a resting to a feeding state ($\beta = -0.11$). Our results indicate that on hunting days geese were less likely to fly and more likely to rest, which contradicts our a priori hypothesis.

On a non-hunting day, with every 1-standard deviation (SD) increase in distance from a blind, geese were less likely to switch from a resting to a flying state ($\beta = -0.34$). On a hunting day, with every 1-SD increase in distance from a blind, geese were even less likely to switch from a resting state to a flying state ($\beta = -0.40 = \beta_{\text{hunt}} + \beta_{\text{blind}} + \beta_{\text{hunt*blind}} = -0.17 + -0.34 + 0.11$). Similarly, the probability of switching from a feeding state to a flying state with every 1-SD increase in distance from a blind on a hunting day ($\beta = -0.37 = \beta_{\text{hunt}} + \beta_{\text{blind}} + \beta_{\text{hunt*blind}} = -0.41 + 0.00 + 0.04$) was less than on a non-hunting day ($\beta = 0.00$). These results support our hypothesis that geese were more likely to switch to a flying state when they were closer to hunting blinds, and hunting further increased those likelihoods.

Likewise, as the number of hunters on the WMA increased geese were more likely to switch to a flying state from a resting state ($\beta = 0.08$) or a feeding state ($\beta = 0.16$). This result supports our a priori hypothesis that geese would be more active when there were more hunters on the WMAs. The effect sizes of each predictor are provided in Table 2-5 and depicted in Figure 2-2.

Table 2-5: Estimated coefficients (β) from hidden Markov models fit to both sites at the fine spatiotemporal scale.

Parameters are listed as the section headers and values indicate how the parameter changes the probability of transitioning from the state listed in the row header to the state listed in the column header. Estimated parameters are on the logit scale.

Hunt Day			
	Resting	Feeding	Flying
Resting	--	-0.11 [^]	-0.17 [^]
Feeding	0.24	--	-0.41
Flying	-0.09 [^]	0.29	--
Distance from Blind			
	Resting	Feeding	Flying
Resting	--	0.04 [^]	-0.34 [^]
Feeding	0.01 [^]	--	0.00 [^]
Flying	0.05 [^]	-0.07	--
Hunt Day x Distance from Blind			
	Resting	Feeding	Flying
Resting	--	-0.02 [^]	0.11 [^]
Feeding	-0.08	--	0.04 [^]
Flying	0.07 [^]	0.14	--
Number of Hunters			
	Resting	Feeding	Flying
Resting	--	0.02 [^]	0.08 [^]
Feeding	-0.07	--	0.16
Flying	0.00 [^]	-0.14	--
Habitat – Grassland			
	Resting	Feeding	Flying
Resting	--	0.33	0.97
Feeding	0.14	--	0.22
Flying	1.36	0.67	--
Habitat – Cropland			
	Resting	Feeding	Flying
Resting	--	-0.05 [^]	2.18
Feeding	-0.28 [^]	--	0.20 [^]
Flying	0.34 [^]	0.14 [^]	--
Habitat – Forest			
	Resting	Feeding	Flying
Resting	--	0.22	0.89
Feeding	-0.19	--	-0.08 [^]
Flying	0.63	0.10 [^]	--

Habitat – Developed			
	Resting	Feeding	Flying
Resting	--	0.94 [^]	-0.04 [^]
Feeding	-1.06 [^]	--	0.68 [^]
Flying	-0.56 [^]	-1.20 [^]	--

[^] Parameter's 98% confidence interval overlaps zero.

Effect of Predictors on Transition Probability

Fine Scale Two-Site Model

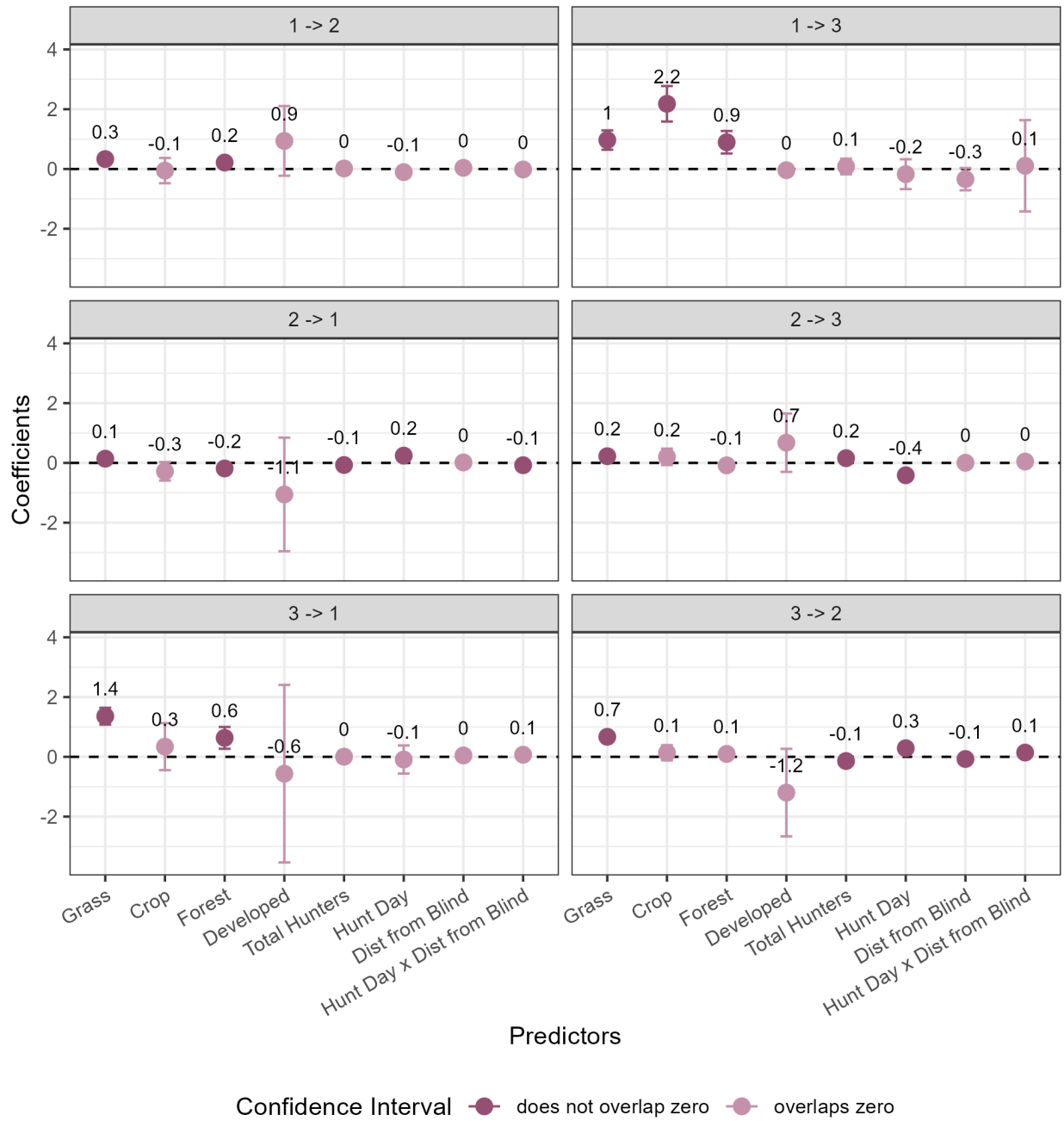


Figure 2-2: Estimated coefficients and associated 98% confidence intervals from hidden Markov model fit to both sites at the fine spatiotemporal scale. Effect sizes are on the logit scale.

Middle Creek Fine Scale

Using data from only Middle Creek, we fit a 3-state model in which one state was interpreted as a ‘resting’ state with $\kappa = 1.48$, $\lambda = 9.08$, and $\mu = 0.07$ rad ($\phi = 0.20$), the second state was interpreted as a ‘feeding’ state with $\kappa = 1.51$, $\lambda = 34.36$, and $\mu = 0.05$ rad ($\phi = 0.13$), and the third state was interpreted as a ‘flying’ state with $\kappa = 0.71$, $\lambda = 167.32$, and $\mu = 0.00$ rad ($\phi = 0.77$).

We estimated that geese were less likely to switch to a flying state from a resting state ($\beta = -0.46$) or a feeding state ($\beta = -0.41$) on a hunting day, which further supports the results from the two-site model and contradicts our a priori hypothesis. Like the two-site model, the Middle Creek model also estimated that on a hunting day as distance from a blind increased geese were less likely to transition to a flying state from a resting state ($\beta = -0.23 = \beta_{\text{hunt}} + \beta_{\text{blind}} + \beta_{\text{hunt*blind}} = -0.46 + 0.07 + 0.16$) or a feeding state ($\beta = -0.91 = \beta_{\text{hunt}} + \beta_{\text{blind}} + \beta_{\text{hunt*blind}} = -0.41 + 0.05 + -0.55$). Additionally, on a non-hunting day, as distance from a blind increased, geese were more likely to switch to a flying state from a resting state ($\beta = 0.07$) or a feeding state ($\beta = 0.05$). These results indicate that, on a non-hunting day, geese were less likely to take flight when closer to a blind, but on a hunting day geese were more likely to take flight when closer to a blind. Further, as the number of hunters at the nearest blinds increased, geese were more likely to take flight from a resting state ($\beta = 0.17$) or a feeding state ($\beta = 0.35$).

Our results also showed that on non-hunting days, geese were less likely to switch to a feeding state from a resting ($\beta = -0.21$) or flying state ($\beta = -0.05$) when farther from a blind. However, on a hunting day, geese were more likely to switch to a feeding state from a flying state when farther from a blind ($\beta = 0.17 = \beta_{\text{hunt}} + \beta_{\text{blind}} + \beta_{\text{hunt*blind}} = 0.21 + -0.05 + 0.01$). This indicates that geese tended to feed closer to blinds on non-hunting days and farther from blinds on hunting days. The effect sizes of each predictor are provided in Table 2-6 and depicted in Figure 2-3.

Table 2-6: Estimated coefficients (β) from hidden Markov models fit to Middle Creek WMA data at the fine spatiotemporal scale.

Parameters are listed as the section headers and values indicate how the parameter changes the probability of transitioning from the state listed in the row header to the state listed in the column header. Estimated parameters are on the logit scale.

Hunt Day			
	Resting	Feeding	Flying
Resting	--	0.16 [^]	-0.46 [^]
Feeding	0.11 [^]	--	-0.41
Flying	-0.17 [^]	0.21 [^]	--
Distance from Blind			
	Resting	Feeding	Flying
Resting	--	-0.21	0.07 [^]
Feeding	0.22	--	0.05 [^]
Flying	0.17 [^]	-0.05 [^]	--
Hunt Day x Distance from Blind			
	Resting	Feeding	Flying
Resting	--	-0.23	0.16 [^]
Feeding	-0.17 [^]	--	-0.55
Flying	-0.01 [^]	0.01 [^]	--
Number of Hunters			
	Resting	Feeding	Flying
Resting	--	-0.02 [^]	0.17 [^]
Feeding	-0.09 [^]	--	0.35
Flying	0.00 [^]	-0.16 [^]	--
Habitat – Cool Season Grasses			
	Resting	Feeding	Flying
Resting	--	0.18 [^]	1.60
Feeding	0.55	--	0.16 [^]
Flying	2.30	1.22	--
Habitat – Warm Season Grasses			
	Resting	Feeding	Flying
Resting	--	-0.31 [^]	1.29
Feeding	0.01 [^]	--	-0.30 [^]
Flying	0.66 [^]	-0.35 [^]	--
Habitat – Corn			
	Resting	Feeding	Flying
Resting	--	-0.24 [^]	2.12
Feeding	-0.75 [^]	--	0.17 [^]
Flying	0.47 [^]	-1.35	--

Habitat – Wheat			
	Resting	Feeding	Flying
Resting	--	-0.80 [^]	2.45
Feeding	-0.28 [^]	--	0.64
Flying	-1.41 [^]	-0.05 [^]	--
Habitat – Hay			
	Resting	Feeding	Flying
Resting	--	-1.51 [^]	-0.59 [^]
Feeding	-0.93 [^]	--	0.36 [^]
Flying	-0.54 [^]	-0.80 [^]	--
Habitat – Forest			
	Resting	Feeding	Flying
Resting	--	0.38	0.40 [^]
Feeding	-0.03 [^]	--	-0.15 [^]
Flying	1.30	0.65	--
Habitat – Developed			
	Resting	Feeding	Flying
Resting	--	0.63 [^]	-0.16 [^]
Feeding	-0.63 [^]	--	-0.59 [^]
Flying	-0.12 [^]	-0.91 [^]	--

[^] Parameter's 98% confidence interval overlaps zero.

Effect of Predictors on Transition Probability

Fine Scale Middle Creek Model

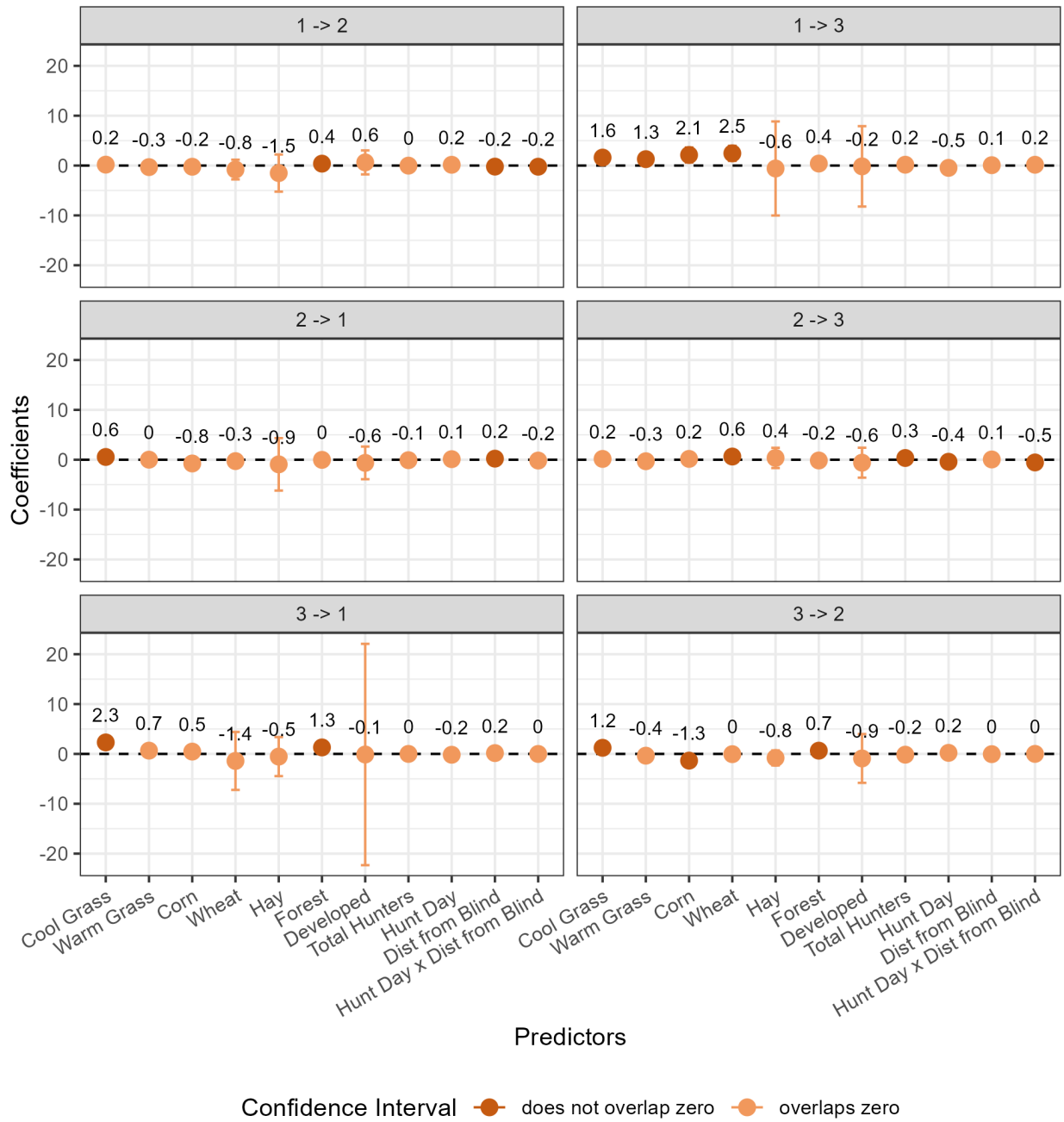


Figure 2-3: Estimated coefficients and associated 98% confidence intervals from hidden Markov model fit to Middle Creek data at the fine spatiotemporal scale. Effect sizes are on the logit scale.

Discussion

We found that geese were less likely to take flight during hunting periods and on hunting days. Notably, hunters shoot at flying geese. Our results did not wholly support our a priori hypothesis that geese would increase their movement rates during hunting, which was based on findings in similar studies of mammalian and avian game species (Cleveland et al., 2012; McDuie et al., 2021; Picardi et al., 2019). Our results suggest that the geese adopted a different risk mitigation strategy than other game species; instead of increasing movement to avoid predation threats, these goose populations decreased their movement. An important difference between this study and similar studies is that these goose populations were exposed to regular (i.e., predictable) bouts of hunting pressure from static locations. It's reasonable that, when the predator is mobile, it is more strategic to rove the landscape in tandem (Mitchell & Lima, 2002), whereas when the predator is immobile the best strategy is to also not move (Cooper et al., 2012). Our finding indicates that the geese maintained both a landscape of fear and a schedule of fear (Laundré et al., 2001; Palmer et al., 2022), which allowed them to employ a proactive behavioral response to a temporally regular and spatially static threat. We also found that, as hunting pressure increased through either proximity to hunting or number of hunters, geese became more likely to move. Geese proactively moved less until the level of threat was proximate enough to elicit a different response, similar to methods adapted by cryptic species (Nishiumi & Mori, 2015), which supports the theory that the magnitude of response will change with the regularity and severity of predation risk (Cromsigt et al., 2013).

When analyzing data from both sites, we found that vigilance behavior, represented by the resting state, increased on hunting days: geese were more likely to switch from feeding to a resting state and less likely to switch from resting to a feeding state. Feeding can be a risky behavior because an individual is focused less on their surroundings and are less likely to notice and evade predation (Makowska & Kramer, 2007; Unck et al., 2009), but increased vigilance can negatively affect body condition and reproductive success because it detracts from foraging (Ciuti et al., 2012; Creel et al., 2014). Additionally, we found that this probability of switching from feeding to a resting (i.e., vigilant) state was less strong as the distance from a hunting blind increased, which supports the predation risk allocation theory that suggests animals will allocate their energy from feeding to vigilance if pulses of predation risk are relatively brief (Lima &

Bednekoff, 1999). Further, at Middle Creek we found that geese were more likely to switch to a feeding state when closer to blinds on non-hunting days but farther from blinds on hunting days, indicating that the geese recognized point sources of predation threats and modified their behavior accordingly (Laundre et al., 2010).

Fear responses can be proactive or reactive and can vary with cycles of spatiotemporal threat (Palmer et al., 2022). Overall, our results suggest that at the current level of hunting pressure geese proactively minimized their predation exposure by moving less on hunting days, which likely involved remaining in areas of spatial refuge. If hunting blinds were redistributed to infringe on and thus limit the current areas of spatial refuge, we might see a different pattern of goose movement (i.e., more flying) in response to hunting (Cleveland et al., 2012; Magle et al., 2014). Our analysis showed that geese were more likely to enter a resting state when on the WMA during both hunting and no hunting, which indicates that the WMAs may serve as a refuge within the broader landscape. However, if blinds disrupt all spatial refuge on the WMAs, we may see geese abandon the WMAs during hunting (Bregnballe & Madsen, 2004). Similarly, we might see a different movement response if the hunting blinds were used selectively throughout the hunting season, thus creating a less predictable landscape of fear (Cleveland et al., 2012; Palmer et al., 2022). Additionally, it's possible that migratory Canada geese would display different movement patterns because they are less familiar with the landscape or are less habituated to anthropogenic disturbance (Thorsen et al., 2022).

Overall, we found that resident Canada geese employed two nested anti-predator behaviors: geese proactively decreased their movement during hunting and increased vigilance, but when proximate to predation threats they were more likely to react by taking flight. Our study provides further evidence that animals maintain a landscape of fear and a schedule of fear (Laundre et al., 2010; Palmer et al., 2022). Carefully managed populations, such as game species, should be provided with sizeable but unpredictable spatial refuge if biologists want to promote both site fidelity and animal movement during hunting.

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Appendix

Chapter 2 Supplemental Figures

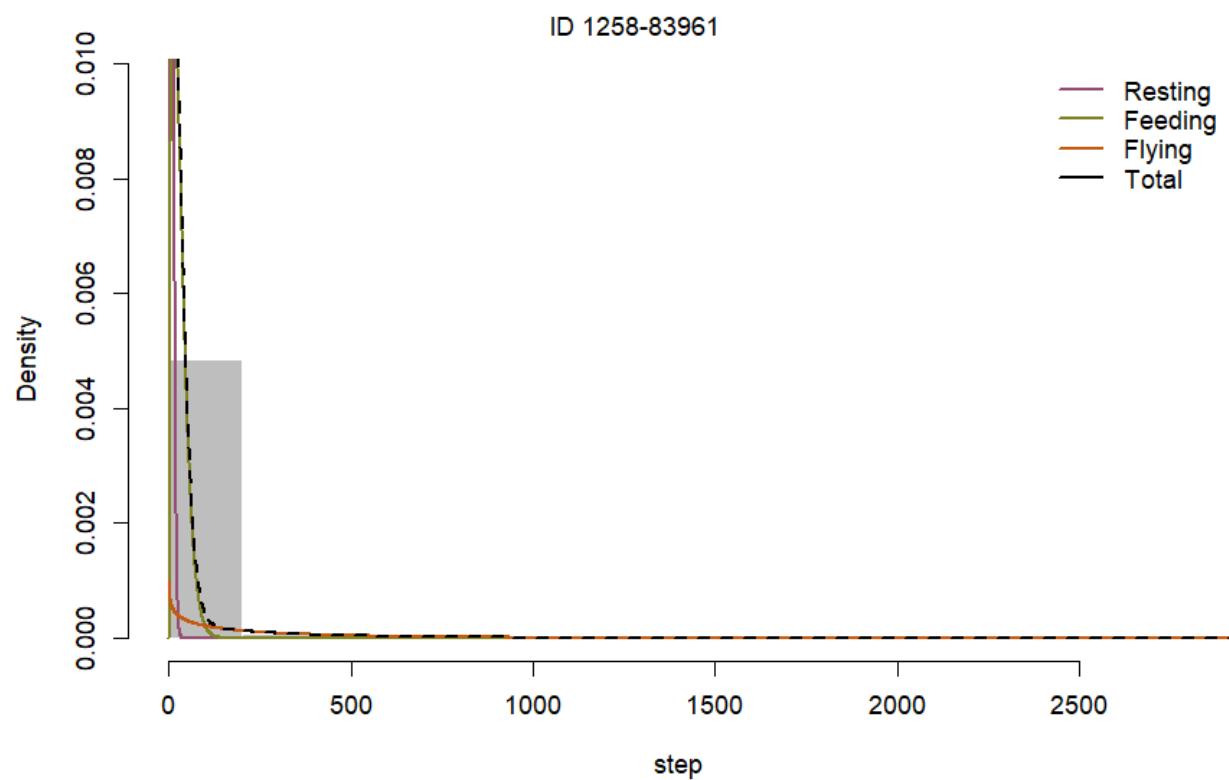


Figure A-1: Fitted step length density for each estimated state plotted over a histogram of one sample individual's step lengths. Each line represents the distribution of step lengths for the corresponding latent state.

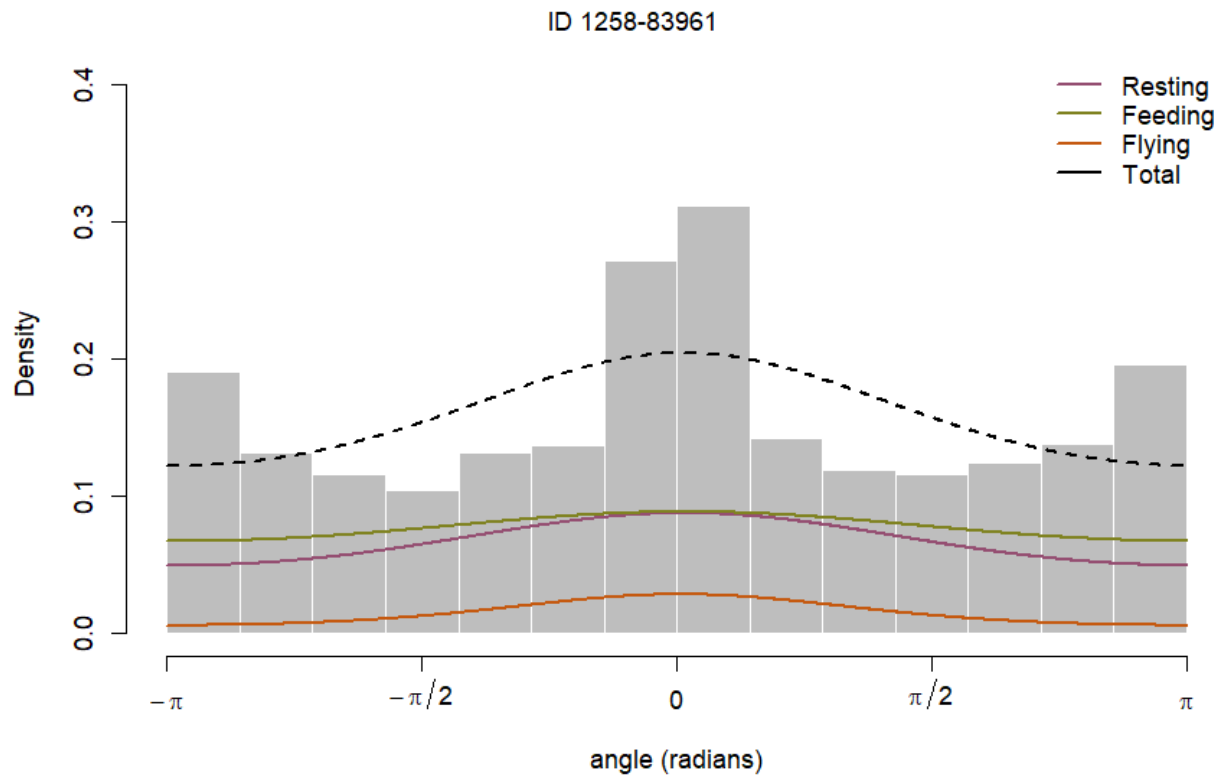


Figure A-2: Fitted turn angle density for each estimated state plotted over a histogram of one sample individual's turn angles. Each line represents the distribution of turn angles for the corresponding latent state.

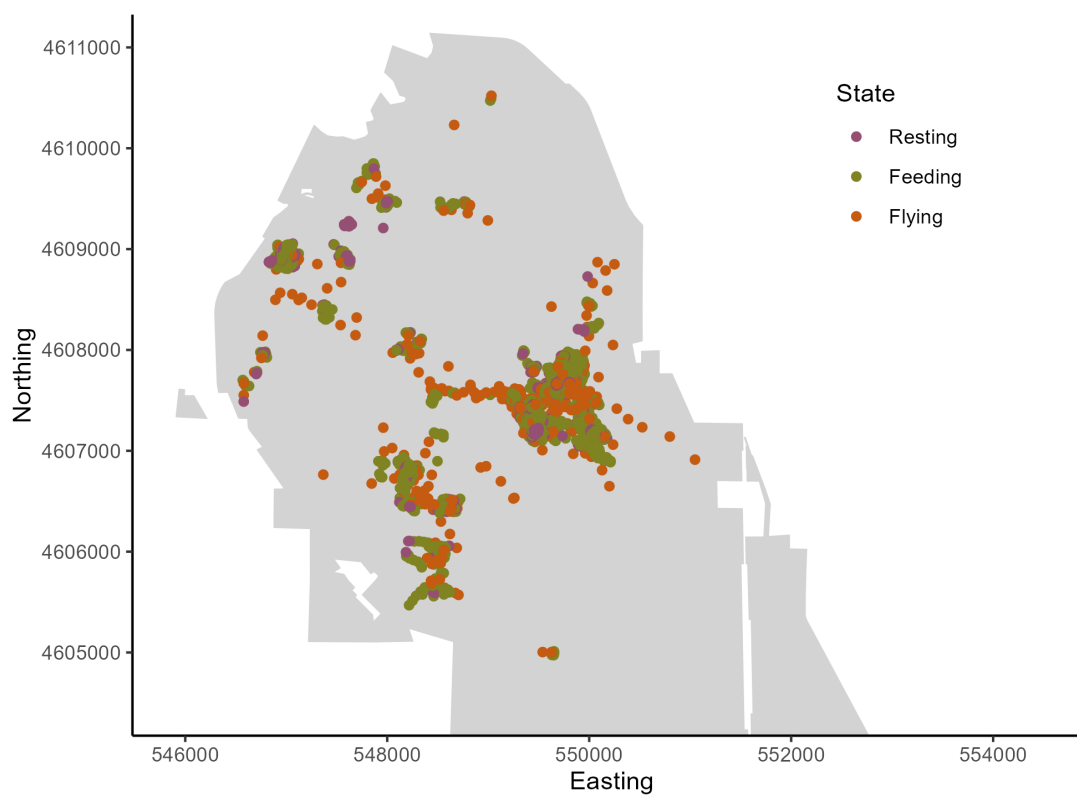


Figure A-3: Most probable state sequence estimated from one individual (ID 1258-83961) at Pymatuning WMA. Each point represents the most likely latent state during that observation within the overall time series.