



Ferruginous Hawk movements respond predictably to intra-annual variation but unexpectedly to anthropogenic habitats

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Birds exhibit flexible movement responses to environmental variation across the annual cycle, and those responses can provide insight into potential impacts that environmental changes may have on these species. To understand year-round variation in space use by Ferruginous Hawks *Buteo regalis*, we tracked 12 birds breeding in southwestern Idaho, USA, using GPS telemetry collected over 207 bird-months. Home-range sizes of territorial adult hawks showed strong intra-annual variation, being smallest from April to June and largest from July to October. In contrast, juvenile birds (< 2 years old) did not appear to hold territories and showed no detectable intra-annual variation in ranging behaviour. Association with land-cover types by territorial birds varied between breeding and non-breeding months and was linked to home-range size. Home-range sizes of non-territorial birds were larger than those of territorial birds, and that size did not vary across the year. Association with anthropogenic habitats (irrigated cropland habitats that can provide high rodent densities and increased foraging opportunities) was negatively associated with home-range size in months of the non-breeding season. Unexpectedly, the opposite was true in the months of the breeding season, such that use of croplands resulted in larger home-ranges. Patterns in home-range size were probably linked to intrinsic factors such as the timing of breeding and migratory behaviour, and to extrinsic factors such as prey availability associated with specific land-cover types. These results have implications for our understanding of the response of Ferruginous Hawks and other similar species to predicted changes in land cover, and they suggest unexpected relationships between human activity and wildlife behaviour. Furthermore, because the birds we tracked used a large portion of western North America, they are probably relevant far beyond the small area where these individuals were trapped.

Keywords: anthropogenic habitats, *Buteo regalis*, Ferruginous Hawk, GPS telemetry, home-range, land-cover association.

Animal movement is driven by a suite of processes acting across a variety of spatial and temporal scales (Nathan *et al.* 2008). For example, across the annual cycle, migratory species travel widely between well-

dispersed areas (Klaassen *et al.* 2014) and even non-migratory animals tend to show intra-annual variation in movement behaviours (van Beest *et al.* 2013). Birds, for example, are exposed to different sets of processes and stressors during breeding, migration and non-breeding periods (Sillett & Holmes 2002). Despite this, monitoring of many

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migratory species is typically limited to only one of these annual periods (Morrison *et al.* 2013, Marra *et al.* 2015). That said, understanding threats and limits to populations throughout the annual cycle is important to guide conservation measures, especially for migratory species (Sillert & Holmes 2002, Klaassen *et al.* 2014, Marra *et al.* 2015, Schuster *et al.* 2019). As such, by collecting movement data on birds, we can begin to understand and manage their interactions with the landscape and climate across large spatial scales (Braham *et al.* 2015, Wilmers *et al.* 2015, Wallace *et al.* 2016, Miller *et al.* 2017, Phipps *et al.* 2019).

Remote tracking has advanced our understanding of the movement ecology of motile species (Kays *et al.* 2015, Katzner & Arlettaz 2020), in part by removing many of the biases associated with historical tracking methods (van Eeden *et al.* 2017). For example, access to resources is a major driver of animal movement behaviour and use of space (Tucker *et al.* 2019) and tracking bias can influence our understanding of resource use (Silva *et al.* 2017). Similarly, home-range, the area where activities such as foraging, breeding and rearing young occur (Burt 1943), is often evaluated to identify habitats relevant to the survival of a species. Therefore, unbiased estimates of intra-annual variation in home-range size can help to inform understanding of which factors are correlated with long-term population stability. Improving home-range estimates during all times of the year is also useful because knowing the size and location of home-ranges can help to assess responses to intra-annual changes to the natural environment. Variation in home-range size can be driven by several factors that allow an animal to meet its energetic and ecological requirements (Burt 1943). For birds, these factors often include availability of food as well as nesting, roosting and perching sites (Miller *et al.* 2017). In some cases, human influence may alter the distribution of these resources in the landscape and provide resources that alter the foraging behaviour, geographical distribution and population dynamics of animals (Hidalgo-Mihart *et al.* 2004, Newsome *et al.* 2015, Petroelje *et al.* 2019, Marcelino *et al.* 2022).

Ferruginous Hawks *Buteo regalis* are diurnal raptors that occupy arid grasslands, shrub-steppe and high-altitude deserts across western North America, from Canada to Mexico (Giovanni *et al.* 2007, Ng *et al.* 2020, 2022). In the Intermountain West region, Ferruginous Hawks are highly dependent on ground squirrels (*Sciuridae* spp.) and other small rodents for

food (Schmutz & Fyfe 1987, Giovanni *et al.* 2007). Like some other raptor species, Ferruginous Hawks have been known to exploit human-altered habitats, such as croplands that support high levels of rodent prey availability (Leary *et al.* 1998, Panek & Hušek 2014, Herring *et al.* 2020). Southern populations of this species may be sedentary or migrate short distances, whereas northern populations are typically medium-distance migrants (Ng *et al.* 2020). Ferruginous Hawk migration is typically non-linear, with birds first migrating longitudinally, possibly responding to variation in rodent abundance, before completing their migration south (Ng *et al.* 2020). This raptor species is classified as vulnerable, imperilled or critically imperilled in 18 of the 21 states and provinces across its range in the United States and Canada (NatureServe 2021), and as a 'Type II Special Status Species' by the Idaho Bureau of Land Management (BLM). In most cases, habitat alteration has been suggested as a possible driver of population declines (Travsky & Beauvais 2005, Ng 2019). As with many species, Ferruginous Hawk ecology has been widely studied during the breeding season but knowledge is limited for other periods of the annual cycle.

We evaluated expectations about animal movement with data collected from Ferruginous Hawks breeding in southwest Idaho, USA. Our overall goal was to better understand patterns of movement ecology and use of space by this species across the annual cycle. Theory predicts that during the nesting season, territorial, breeding individuals should use less space than non-breeders, that animals may vary their movements in response to anthropogenic habitats, and finally that movement behaviour should respond to intra-annual variation in both internal and external factors (e.g. cycles in breeding behaviour and availability of food resources). To test these predictions, we estimated variation in home-range size of Ferruginous Hawks across months and in response to potential intrinsic (sex, age) and extrinsic (land cover and seasonal) drivers.

METHODS

Study site

We studied Ferruginous Hawks that nested or hatched within the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA), in the state of Idaho, USA (Fig. 1a). Historically the NCA was dominated by *Artemisia* spp. shrub-steppe. However, due to wildfires, much of the

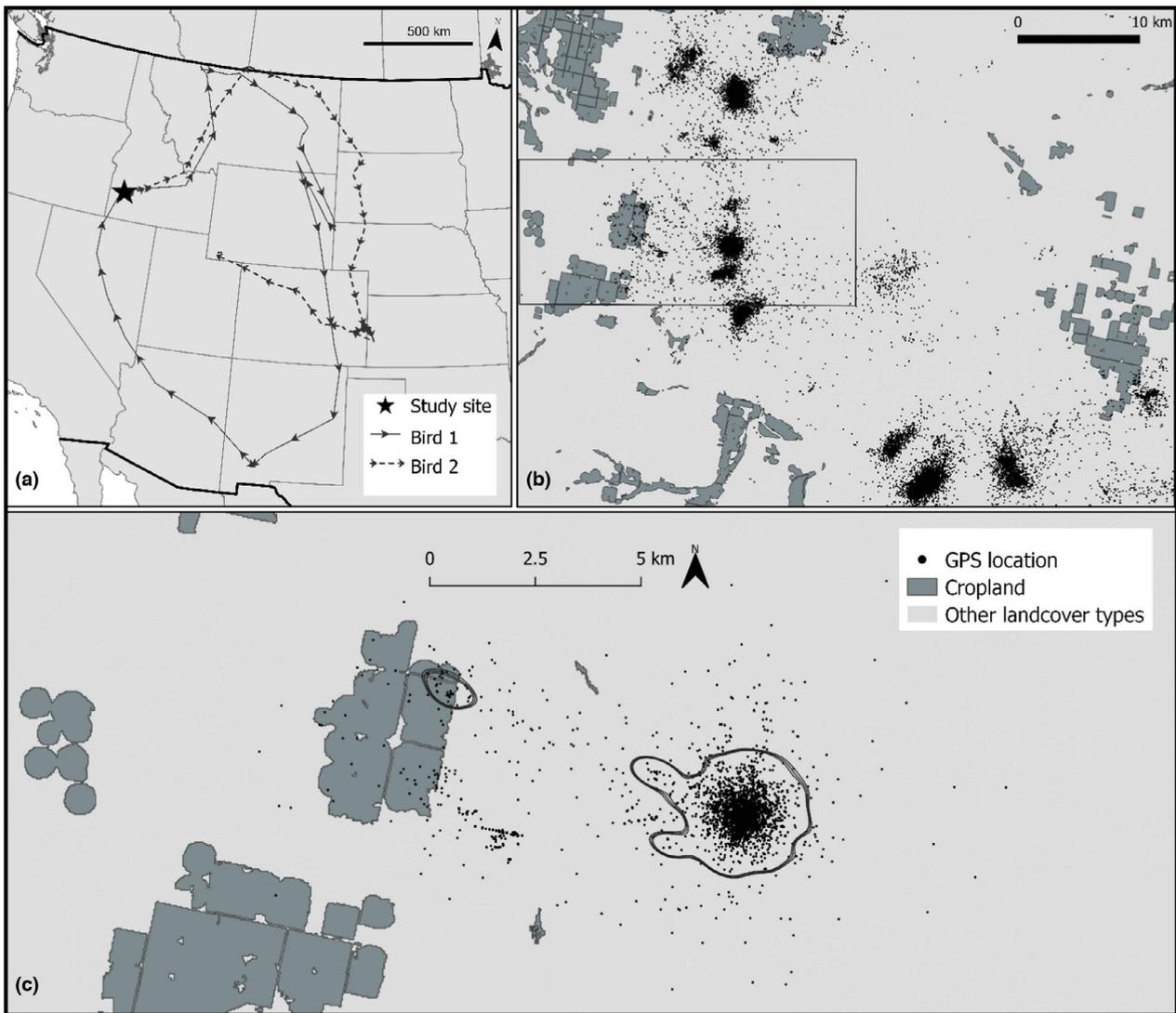


Figure 1. (a) GPS locations of two Ferruginous Hawks (solid and dashed black lines) tracked from breeding locations in southwest Idaho for one full annual cycle across North America. Both birds initially moved north from breeding grounds following the direction of the arrows. Star symbol indicates the capture site at the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA), Idaho. (b) GPS fixes of all individuals ($n = 12$) tracked throughout their breeding area in the NCA. Dark grey patches show the distribution of cropland and black box shows area in (c), data from a single individual tracked throughout the NCA during one breeding season, illustrating this bird's main area of use around the nest, with excursions to those croplands. Black lines indicate the autocorrelated kernel density estimate of home-range boundary with 95% confidence intervals for 1 month of movement.

NCA has been converted to open habitats dominated by native grasses and exotic annuals (Pilliod *et al.* 2017). Agricultural practices have also altered the landscape, with 5–6% of the NCA containing irrigated croplands (Stuber *et al.* 2018). At this site, Ferruginous Hawks typically arrive on territories during March before laying eggs in mid-April (Howard 1975). Nestlings typically fledge in June and all birds depart from the natal site, usually travelling to Canada, in late July–August.

Capture and GPS data collection

We considered two age-classes of birds: free-flying territorial adults captured near nests (hereafter adults) and non-territorial first- and second-year birds captured as non-flighted nestlings (hereafter juveniles). No birds captured as nestlings were observed to hold a breeding territory.

To capture free-flying Ferruginous Hawks, we used mist-nets and a robotic Great Horned Owl

Bubo virginianus lure placed near the nest (Jensen *et al.* 2019). We captured nestlings by hand in the nest or on the ground immediately after fledging. Birds were fitted either with 30-g CTT-1030-BT3 Series GPS-GSM telemetry devices (Cellular Tracking Technologies, Rio Grande, NJ, USA) or 22-g Argos/GPS solar-powered Platform Transmitter Terminal (PTT; Microwave Telemetry, Inc., Columbia, MD, USA; Bird & Bildstein 2007). We attached transmitters with Teflon ribbon in a backpack-style harness and followed published guidelines ensuring that the mass of the telemetry unit and harness was not > 3% of the bodyweight of the animal (Steenhof *et al.* 2006, Bird & Bildstein 2007). The GPS-GSM units were programmed to collect GPS locations, altitude, speed, fix quality (2D or 3D fix), and horizontal and vertical dilution of precision (HDOP and VDOP) at 15-min intervals during daylight hours throughout spring, summer and autumn months. During winter, interval length was increased (up to 6 h) due to reduced solar energy limiting recharging of batteries. The Argos-PTT units were programmed to collect GPS locations, altitude, speed and fix quality at 3-h intervals, year-round.

Data collected were sent to a server via the GSM mobile phone network once per day, or via Argos satellites several times per week. Prior to analysis we removed poor quality GPS points indicated by 2D fix quality (Poessel *et al.* 2018). For GPS-GSM units, we also removed points for which the horizontal or vertical dilution of position (HDOP or VDOP) was > 10 (D'Eon & Delparte 2005). We calculated user equivalent range errors (UEREs) from GPS points collected while devices were in a static position for a period of 17–30 days using the *ctmm* package in R (GPS-GSM UERE: horizontal = 1.76; vertical = 3.08; PTT UERE: horizontal = 2.25; vertical = 1.97; Noonan *et al.* 2019; R Core Team 2021). We calculated the start and end of the daylight period for each GPS location using the *suncalc* package in R (Thieurmél & Elmarhraoui 2019, R Core Team 2021) and we excluded fixes that were collected after sunset but before sunrise.

Monthly home-range size and land cover

We estimated home-range area for each bird in each month, using autocorrelated kernel density estimators (AKDEs) implemented in the *ctmm* package in R (Fleming *et al.* 2015, Calabrese *et al.* 2016, R Core Team 2021). AKDEs

incorporate movement effects by fitting models to GPS data to estimate an autocorrelation structure. Calculating bird home-range for each month allowed us to evaluate changes in home-range size throughout the annual cycle, as well as to compare home-range size between seasons. AKDEs are also useful because they control for irregular and uneven sampling rates. We calculated individual home-ranges for birds captured as juveniles once they settled (see below) > 100 km from their nest-site (typically after August). All periods of migration, including short migratory stopovers, were excluded from any analysis.

The *ctmm* package requires range residency to calculate home-ranges. Therefore, prior to any analysis, we determined range residency using visual checks for asymptotic behaviour of semi-variograms produced by the *ctmm* package (Calabrese *et al.* 2016). We identified and removed outlier telemetry locations using the *outlie()* function in *ctmm* and the associated core deviation and speed plots (Noonan *et al.* 2019). We only estimated home-range for bird-months where birds were range resident for ≥ 8 days and with ≥ 30 GPS points (Braham *et al.* 2015; Fig. 2b). During those months where birds were only partially range resident (i.e. spent a portion of the month wandering), we estimated home-range using only the days when the bird was range resident. When birds established range residency in more than one area within the same month, we used the separate home-range estimates to calculate a mean that we weighted by the duration spent in each home-range.

We used the *variogram.fit()* function in *ctmm* to identify starting values for model parameters (following Calabrese *et al.* 2016; see below for description of parameters). The *ctmm* package allows testing models with a suite of different distributional assumptions. Therefore, for each bird-month, we fit and compared all possible movement models available in this package (see Calabrese *et al.* 2016 for details of the different movement models available in the *ctmm* package). We selected the most appropriate model via the Akaike information criterion corrected for small sample sizes (AICc). We then calculated the final 95% ADKE using the movement model with the lowest AICc value for that bird-month.

We assessed land-cover association within home-ranges across the annual cycle. To characterize land-cover types within each home-range, we imported into R the home-ranges and associated

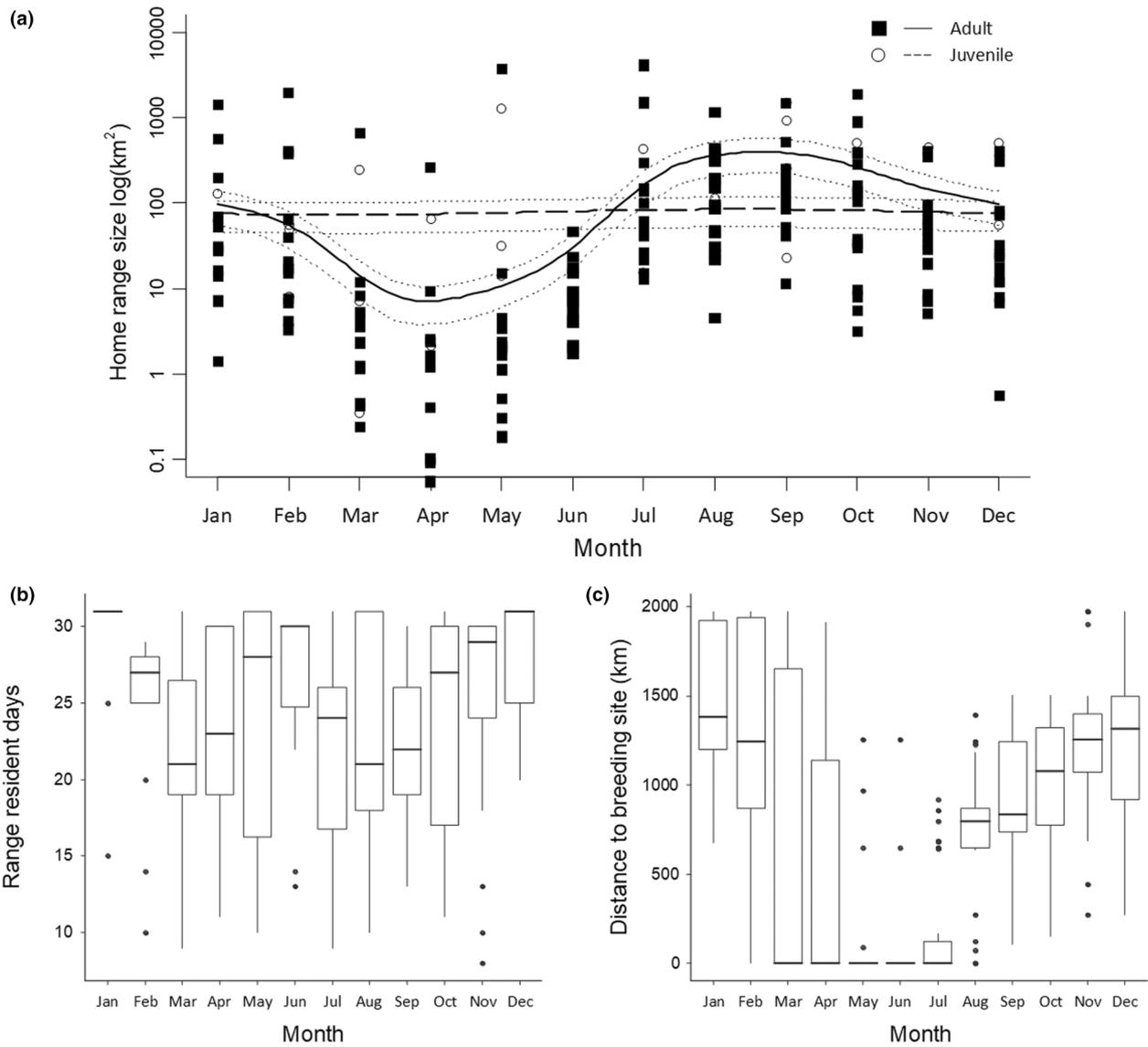


Figure 2. (a) Generalized additive mixed model and 95% confidence intervals showing effect of month on mean monthly home-range of Ferruginous Hawks (95% autocorrelated kernel density estimation, $n = 12$ hawks (eight captured as adults, four captured as juveniles) and 207 bird-months) tracked between 2016 and 2021 in North America. (b) Number of days analysed where birds were range resident for each month. (c) Distance of home-range areas from the breeding site (NCA) for each month analysed.

land-cover information from the 2015 North American Land Cover dataset, which has a resolution of 30 m² (Commission for Environmental Cooperation 2015). We then used the raster package (Hijmans *et al.* 2021) to calculate the proportion of each land-cover type (Barren, Cropland, Temperate Grassland, Temperate Shrubland, Urban, Water, Wetland, Forest, Tropical Grassland and Tropical Shrubland) within each home-range.

Statistical modelling

We evaluated intra-annual (monthly) variation in home-range size throughout the year using a generalized additive mixed model (GAMM; R package mgcv; Wood *et al.* 2016). Fixed effects in the model were age and sex, and random effects were individual bird identity. We tested model performance with and without a random effect for year,

to account for response of birds to year-to-year variation. We fitted a cyclic smoothing spline to the month term in the model to capture non-linear relationships associated with this term. As our data were continuous and zero-bounded, we used the Gamma error family with a log link function. As the timing of migration by these hawks was variable, we evaluated seasonal variation in home-range size during months where birds were exclusively within the breeding range or winter ranges using a generalized linear mixed effects model (GLMM; lme4 package in R; Bates *et al.* 2015). The fixed effect in the model was season (3 months each, either breeding (April–June) or wintering (November–January)). Random effects were individual bird identity and year. We again used the Gamma error family with a log-link function.

We evaluated the relationship between home-range size and land-cover types within those home-ranges with two GLMMs. We built separate models for the months in which we had breeding (March–July) and non-breeding (August–February) season home-ranges (these are slightly different months from those in the prior analyses because this analysis included short periods of residency in autumn). For the breeding season, we included fixed effects for proportions of two land-cover types, cropland and grassland (as defined by the 2015 North American Land Cover dataset noted above). During the breeding season, three land-cover types – cropland, grassland and shrubland – were most widely available within home-ranges. Shrubbyland was excluded as a fixed effect, as values of this variable were highly positively correlated with grassland. Bird identity again was included as a random effect in the model. For months spent exclusively in the breeding territory (April–June), we also used a linear regression to test the relationship between mean home-range size of birds and distance from the nest to the nearest cropland.

When not on breeding grounds, land-cover types present within home-ranges were highly variable among birds, and, within home-ranges, we detected correlations in proportional cover of many land-cover types. As such, to focus on the role of anthropogenic habitats on birds, we included in our models only one fixed effect, proportion of cropland, with bird identity as a random effect. In both models, we again used the Gamma error family with a log-link function.

RESULTS

We considered GPS data from 12 Ferruginous Hawks, eight adults (five female and three male) and four juveniles (two female and two male), captured in the NCA during May–June 2016–2019, and tracked over the subsequent months (Supporting Information Table S1). Over the study period (May 2016 to April 2021) we collected 185 941 high-quality GPS locations during daytime (Fig. 1b). The duration of tracking for individual birds ranged from 1 to 45 months. After removing bird-months for which data were sparse, we estimated home-ranges for 207 bird-months (details on sample sizes by month are provided in Supporting Information Table S2).

Monthly home-range size and landscape predictors

The monthly 95% home-range sizes of Ferruginous Hawks varied across the entire annual cycle and ranged from 0.06 to 4085.41 km², averaging 191.39 ± 34.37 km² (\pm se; $n = 12$ birds and 207 bird-months; Fig. 1c, Supporting Information Table S3). Monthly home-range size of adults during the breeding season (March–July) ranged from 0.01 to 3723.59 km² (115.81 ± 55.94 ; $n = 10$ birds and 76 bird-months), and outside of the breeding season (August–February) from 0.55 to 4085.41 km² (223.96 ± 50.05 ; $n = 9$ birds and 106 bird-months). Monthly home-range size of juveniles during the breeding season ranged from 0.35 to 1295.43 km² (207.70 ± 158.03 ; $n = 3$ birds and 8 bird-months). Monthly home-range size of juveniles outside of the breeding season ranged from 7.97 to 1476.34 km² (318.49 ± 94.46 ; $n = 4$ birds and 17 bird-months).

There was a non-linear association between month and average home-range size (i.e. the spline of month was highly significant for adult hawks; effective degrees of freedom (edf) = 4.94, ref df = 8, $F = 14.71$, $P < 0.001$; Fig. 2a) but not for juvenile birds (edf = 0.71, ref df = 8, $F = 0.13$, $P = 0.22$; Fig. 2a). Home-range size of adult Ferruginous Hawks was smallest during the breeding season months of May (2.59 ± 1.01 km², $\bar{x} \pm$ se, $n = 8$ birds and 15 bird-months), June (9.65 ± 2.26 km², $n = 10$ birds and 21 bird-months) and April (24.94 ± 23.18 km², $n = 8$ birds and 13 bird-months; Fig. 2a). In contrast, empirical means of

home-ranges were largest during July ($412.52 \pm 216.78 \text{ km}^2$, $n = 9$ birds and 20 bird-months) and October ($277.54 \pm 119.50 \text{ km}^2$, $n = 9$ birds and 19 bird-months; Fig. 2a). Overall, home-range size in the 3 months of the breeding season (April–June) was significantly smaller than during the 3 months of the wintering season (November–January; $P < 0.001$). Monthly home-range size of Ferruginous Hawks was not different among the sexes ($P = 0.46$; Table 1). Including a random effect for year reduced model performance and so we did not consider this term in our modelling efforts.

There were six land-cover types within the home-ranges we estimated for the months between March and July (when known, arrival and departure dates to and from the breeding ground were 5 January to 21 March and 11–28 July, respectively; Fig. 2c). The most abundant land-cover types were Temperate Grasslands ($\bar{x} = 58.24\%$), Temperate Shrublands ($\bar{x} = 40.98\%$) and Croplands ($\bar{x} = 0.68\%$; Table S4a). When on non-breeding range (arrival dates on non-breeding grounds ranged from 16 July to 21 February and departure dates ranged from 27 December to 5 March; Fig. 2c), Ferruginous Hawks were range resident in a huge diversity of areas ($n = 47$ home-range areas spanning from 26.138° to 51.285°N latitude) throughout the USA, Mexico and Canada. Within those home-ranges there were 12 land-cover types available in the landscape, with Temperate Grasslands and

Croplands being most abundant ($\bar{x} = 46.48\%$ and $\bar{x} = 36.14\%$, respectively; Table S4b).

Cropland was an exceptionally good predictor of variation in monthly home-range size of Ferruginous Hawks. During the nesting season, although hawks were only associated with small amounts of cropland, this cover type was strongly positively associated with monthly home-range size ($\beta = 37.01$, $t = 4.51$, $P < 0.001$; Table 1, Figs 1c and 3a). There was a weak positive correlation between monthly home-range size of adult birds during the breeding season months and distance to the nearest area of cropland ($r = 0.36$; $P = 0.153$). Grassland was also positively associated with home-range size during the breeding season ($\beta = 3.84$, $t = 3.33$, $P < 0.001$; Table 1). In contrast, outside of the breeding season, hawks were associated with larger quantities of cropland, but this cover type was strongly negatively associated with home-range size ($\beta = -1.86$, $t = -3.35$, $P < 0.001$; Table 1, Fig. 3b).

DISCUSSION

It is not surprising that the home-range of these hawks varied across the annual cycle, and these types of responses have been widely documented in the literature (e.g. Braham *et al.* 2015, Miller *et al.* 2017). General movement behaviour of our hawks was also similar to that reported previously

Table 1. Models evaluating variation in size of home-ranges of Ferruginous Hawks from the Morley Nelson Snake River Birds of Prey National Conservation Area, Idaho, 2016–2021. Generalized additive mixed models were run to explain the influence of (a) sex and month on home-range size (monthly 95% autocorrelated kernel density estimation (AKDE), $n = 12$ hawks and 207 bird-months). Generalized linear mixed-effects models were used to explain influence of (b) season on home-range size (95% AKDE) of breeding adult hawks; and the influence of land-cover type on monthly home-range size (95% AKDE) of (c) territorial Ferruginous Hawks during the breeding season ($n = 8$ hawks and 58 bird-months); (d) and all hawks during the non-breeding season ($n = 11$ hawks and 119 bird-months). Sex comparisons use female as the reference level.

Response	Predictor	df/edf	Estimate	se	t-value	P-value
(a) Home-range size	Intercept	1	4.56	0.41	11.00	<0.001
	Sex	1	-0.53	0.72	-0.74	0.46
	Month Adult	4.94				<0.001
	Month Juvenile	0.71				0.22
(b) Seasonal home-range size	Intercept	1	1.52	0.28	5.39	<0.001
	Winter	1	2.71	0.33	8.27	<0.001
(c) Home-range size (Breeding season)	Intercept	1	-0.71	0.81	-0.88	0.38
	Cropland	1	37.01	8.20	4.51	<0.001
	Grassland	1	3.84	1.15	3.33	<0.001
(d) Home-range size (Non-breeding season)	Intercept	1	5.75	0.30	19.83	<0.001
	Cropland	1	-1.86	0.56	-3.35	<0.001

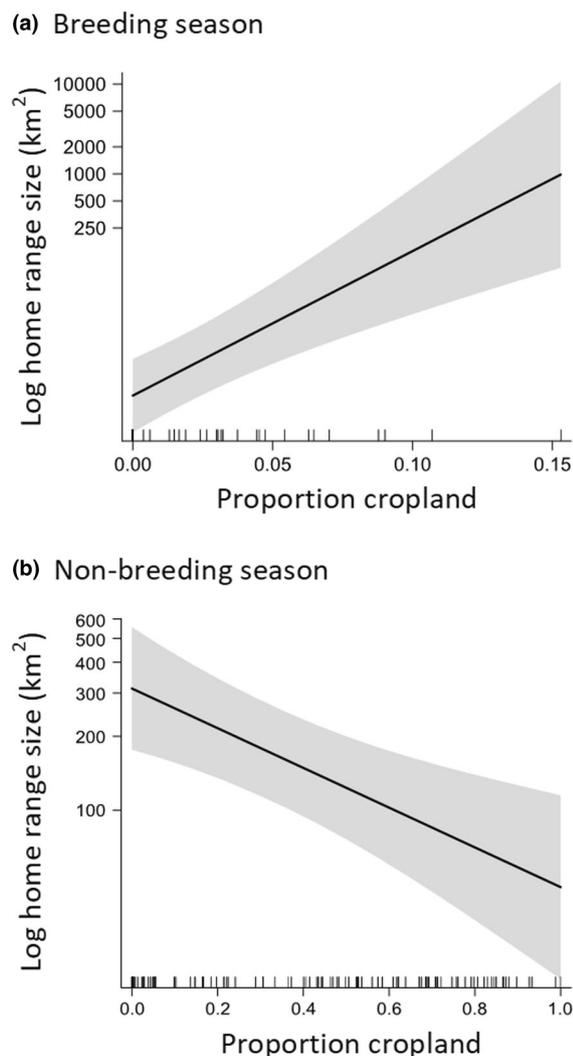


Figure 3. Effects of proportion of cropland within the home-range (95% autocorrelated kernel density estimation) on home-range size of Ferruginous Hawks inside and outside of the breeding season. (a) Breeding adult hawks during the breeding season (March–July) and (b) range resident hawks outside of the breeding season (August–February). The shaded area represents the 95% confidence interval around home-range size.

for this species (Leary *et al.* 1998, Watson 2003, Watson 2020, Kocina & Aagaard 2021). In contrast, although movement responses of wildlife to anthropogenic habitats have also been well studied (Lanszki *et al.* 2018, Main *et al.* 2020, Todorov *et al.* 2020), the seasonal variation we observed in movements in relation to cropland was unexpected. The contrast between these expected and unexpected movement patterns thus provides important insight into the drivers of movement for

these and other species which may select for anthropogenic habitats.

Documenting the expected

Ranging behaviour of animals is expected to respond to intrinsic factors such as age, sex and breeding status, as well as extrinsic factors such as seasonality and resource availability. Our analyses tested for both types of factors. The patterns we observed, with the smallest home-ranges during the months of the breeding season and larger home-ranges at other times of year, fit our expectations for how territorial and migratory species typically behave. Similar to other raptor species, adult Ferruginous Hawks appeared as central place foragers that stay close to the nest-site during breeding months, presumably to defend their territory and rear their young (Watson 2003, 2020, Moss *et al.* 2014, Miller *et al.* 2017, Ng *et al.* 2020). In contrast, and again consistent with our expectations, younger and apparently non-territorial hawks were not tied to a specific nesting site and therefore had larger home-ranges. Although we restricted analyses to periods of residency, larger home-ranges of non-territorial birds may still be associated with a higher degree of local wandering and exploration for potential breeding sites (Miller *et al.* 2017, Watson *et al.* 2019, McCabe *et al.* 2021). The larger home-ranges we observed outside of the breeding season could have been linked to reduction in habitat quality due to changes in factors such as prey availability (Moss *et al.* 2014, Mirski *et al.* 2021) or a reduction in defensive behaviour and sharing of resources (Grande *et al.* 2009).

There are two notable caveats to our inference regarding response to these resources. First, we were not able to test how variation in food availability between years may have influenced movement of these hawks. We expect that during years with less abundant food resources, home-range sizes would be larger. Secondly, we did not detect sex-specific differences in home-range size of these birds. Such differences have been detected for some adult raptors (female Red Kites *Milvus milvus* and Golden Eagles *Aquila chrysaetos* have larger home-ranges than did the males; Braham *et al.* 2015, Spatz *et al.* 2022; male Montagu's Harriers *Circus pygargus* have larger home-ranges than do the females; Krupiński *et al.* 2021) but not for others (Golden Eagles in Miller *et al.* 2017). In this

case, it is unclear exactly what factors may have resulted in the lack of sex-related differences in ranging behaviour.

Documenting the unexpected

Animals sometimes travel long distances to reach specific natural resources. For example, African elephants *Loxodonta* spp. and other mammals travel to access essential minerals found in salt licks (Lameed & Adetola 2012). Similarly, bats are known to travel long distances through landscapes dominated by cropland to access sparsely distributed patches of natural woodland or riparian habitats (Kniowski & Gehrt 2014). However, it is less commonly documented that those increases in movements are motivated by anthropogenic habitats, as we observed here. In fact, anthropogenic habitats often result in a contraction of home-ranges, as animals restrict their movements to utilize small patches of the landscape with atypically dense resource availability (Petroelje *et al.* 2019). In a similar vein, Red Kites in the UK may travel away from roosts and breeding sites to forage at locations where supplementary feeding occurs (Orros & Fellowes 2015).

The territorial Ferruginous Hawks we studied frequently visited small parcels of irrigated cropland. However, as noted previously in south-central Washington during the breeding season (Leary *et al.* 1998), they travelled surprisingly long distances to access those parts of the landscape. This increased the size of their home-ranges. Irrigated croplands provide perches, low vegetation density and high rodent populations for some raptors during certain parts of the year (Panek & Hušek 2014, Ng 2019, Zagorski & Swihart 2021). As Ferruginous Hawks are rodent specialists (Schmutz & Fyfe 1987, Giovanni *et al.* 2007, Ng 2019), we suspect that the cropland they were using may be an anthropogenic subsidy for these birds. Specifically, we suspect that they were exploiting agricultural areas with high-density prey populations or increased hunting opportunities, as has been seen for other raptors (Panek & Hušek 2014, Herring *et al.* 2020). All that said, our analyses and understanding of key data on crop type, levels of irrigation and foraging success are insufficient to draw strong inferences in this regard.

The explanation for this atypical behavioural response to an anthropogenic habitat may lie in the details of the breeding biology for this species and

specific features of our study site. Ferruginous Hawks are, in general, nest-site limited (Wallace *et al.* 2016). Typically, these birds build nests on natural substrates such as trees and cliffs or on elevated anthropogenic structures, although they may also nest on the ground where elevated sites are not available (Wallace *et al.* 2016, Ng *et al.* 2020). In our study area, land managers have created a large number of artificial nesting platforms that were used by all the territorial Ferruginous Hawks that we tagged. Furthermore, only some of these platforms are located near agricultural lands. That said, nearly all of the hawks that we tracked made trips, apparently for foraging, to agricultural habitats (Fig. 1b,c). Therefore, the desire to use two anthropogenic resources, nesting platforms and croplands, probably created the atypical response that we observed, with most birds accessing croplands, whether their nest platform was close to or far from that cover type. The fact that they sometimes did not use the closest agricultural landcover also probably explains why we only detected a weak relationship between distance to cropland and home-range size.

This proposed explanation for the atypical response to cropland we observed also helps us to understand why the hawks we studied showed the more typical pattern in winter, having smaller home-ranges when centred on agriculture. Winter habitat of Ferruginous Hawks includes the edges of agricultural land which support an abundance of rodent prey (Watson 2003, Ng *et al.* 2020). During the non-breeding season, these hawks have no need for artificial nest platforms and thus, unlike in the nesting season, their movements are exclusively in response to a single anthropogenic resource. Understanding how Ferruginous Hawks show intra-annual change in their response to cropland therefore provides important insight into the nuance of this human-wildlife interaction. It may therefore be useful to ask whether this nuance extends to other species of conservation concern, particularly those which simultaneously utilize more than one anthropogenic resource.

Improper placement of artificial nesting structures may result in structures remaining unoccupied or being associated with low productivity (Catry *et al.* 2011, Gottschalk *et al.* 2011). For Ferruginous Hawks, and other species which utilize these nesting platforms, it may therefore be beneficial to construct platforms closer to the habitats in which they are exploiting resources. This

pattern will probably hold true for other raptor species that specialize on rodent prey and that are associated with cropland. In our study area, such species may include Red-tailed hawks *Buteo jamaicensis* and Swainson's Hawks *Buteo swainsoni* (Coates et al. 2014). However, it should be noted that not all types of croplands will impact raptors in the same way (Assandri et al. 2022). Furthermore, although the cropland in our study appeared to allow hawks to forage successfully during breeding season months, crops that increase in height and density over the course of a season may reduce the ability of hawks to catch prey (Panek & Hušek 2014, Rodríguez et al. 2014).

CONCLUSIONS

This is said to be a golden age of animal movement studies (Kays et al. 2015). Although Ferruginous Hawks are widespread in western North America, their biology is poorly understood. The novel tracking technologies we deployed to track these birds, in combination with detail on the environment they occupied, provided new insight into their behaviours. Most, but not all, of the relationships we documented were those that theory would predict and were consistent with previous study of this species. The unexpected behaviours therefore provide important insight into how Ferruginous Hawks prioritize resources on the landscape and how human activity, in this case providing two simultaneous resources, can influence the ecology and movements of these and potentially other wildlife adapting to anthropogenic alterations to the landscape.

A large number of people assisted in work to trap and telemeter the hawks studied in this project. Terry Bennet manufactured the mechanical owl used in trapping. Steve Alsup, Joe Weldon, Talia Jolley, Jamie Yurick, Ariana Dickson and many others provided crucial information on nest occupancy. James Belthoff played a crucial role in organizing the university placement that made this research possible. The Katzner lab provided feedback on early versions of the manuscript. J. Ng, an anonymous reviewer, associate editor W. Vansteelant and editor R. Kimball provided useful reviews of the manuscript. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

AUTHOR CONTRIBUTIONS

Georgia Holly Isted: Conceptualization; formal analysis; writing – original draft, writing – review and editing. **Robert J. Thomas:** Conceptualization; formal analysis; supervision; writing – original draft, writing – review and editing. **Kevin S. Warner:** Data curation, funding acquisition; methodology; writing – review and editing. **Matthew J. Stuber:** Data curation, funding acquisition; methodology; writing – review and editing. **Ethan Ellsworth:** Funding acquisition; writing – review and editing. **Todd Katzner:** Conceptualization; data curation, formal analysis; funding acquisition; methodology; supervision; writing – original draft, writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICAL NOTE

This research was conducted under IACUC protocol #006-AC18-003 from Boise State University and #14-0303 from West Virginia University, and complies with the Guidelines to the Use of Wild Birds in Research. Research was conducted under U.S. Federal Bird Banding Permit #23715 and Idaho Wildlife Collection Permit #110728.

Data Availability Statement

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Additional details on individual birds tracked from the Morley Nelson Snake River Birds of Prey National Conservation Area, Idaho, USA, across their annual cycle in North America. Age is at capture, free-flying adults were captured at the nest and tagged, and juveniles were captured as nestlings in the nest. Tracking duration is from the day of capture until the transmitter stopped functioning or the bird died. Transmitters either send data over the mobile phone network (GSM) or the Argos satellite system (PTT).

Table S2. Number of Ferruginous Hawks (auto-correlated kernel density estimation; AKDE) home-ranges (95%) used to estimate mean monthly home-range size by month over the period 2016–2021.

Table S3. Monthly estimates of home-range size for Ferruginous Hawks tagged in Idaho, USA, between 2016 and 2021. Estimates are by bird and month of year. Free flying adults were captured at the nest and tagged, and juveniles were captured as nestlings in the nest. Transmitters either send data over the mobile phone network (GSM) or the Argos satellite system (PTT). Home-range size, 95%, was estimated with AKDE in ctm (see details in main manuscript). This approach requires range residency, and we report the number of days of range residency in each month (period of range residency was 8–31 days). Also reported is the proportion of the home-range composed of cropland land cover (see text for details).

Table S4. Average home-range size and percentages of land cover types used by individual Ferruginous Hawks inside and outside of the breeding season across North America from 2016 to 2021. Home-ranges are a mean of three-monthly estimates across each season.