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Drivers of site fidelity in ungulates

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Abstract

1. While the tendency to return to previously visited locations—termed 'site fidelity'—is common in animals, the cause of this behaviour is not well understood. One hypothesis is that site fidelity is shaped by an animal's environment, such that animals living in landscapes with predictable resources have stronger site fidelity. Site fidelity may also be conditional on the success of animals' recent visits to that location, and it may become stronger with age as the animal accumulates experience in their landscape. Finally, differences between species, such as the way memory shapes site attractiveness, may interact with environmental drivers to modulate the strength of site fidelity.
2. We compared inter-year site fidelity in 669 individuals across eight ungulate species fitted with GPS collars and occupying a range of environmental conditions in North America and Africa. We used a distance-based index of site fidelity and tested hypothesized drivers of site fidelity using linear mixed effects models, while accounting for variation in annual range size.
3. Mule deer *Odocoileus hemionus* and moose *Alces alces* exhibited relatively strong site fidelity, while wildebeest *Connochaetes taurinus* and barren-ground caribou *Rangifer tarandus granti* had relatively weak fidelity. Site fidelity was strongest in

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predictable landscapes where vegetative greening occurred at regular intervals over time (i.e. high temporal contingency). Species differed in their response to spatial heterogeneity in greenness (i.e. spatial constancy). Site fidelity varied seasonally in some species, but remained constant over time in others. Elk employed a 'win-stay, lose-switch' strategy, in which successful resource tracking in the springtime resulted in strong site fidelity the following spring. Site fidelity did not vary with age in any species tested.

4. Our results provide support for the environmental hypothesis, particularly that regularity in vegetative phenology shapes the strength of site fidelity at the inter-annual scale. Large unexplained differences in site fidelity suggest that other factors, possibly species-specific differences in attraction to known sites, contribute to variation in the expression of this behaviour.
5. Understanding drivers of variation in site fidelity across groups of organisms living in different environments provides important behavioural context for predicting how animals will respond to environmental change.

KEYWORDS

familiarity, habitat selection, learned behaviour, memory, migration, past experience, philopatry, predictability

1 | INTRODUCTION

Mobile animals often have strong tendencies to return to previously visited sites (Piper, 2011). This behaviour—here termed 'site fidelity'—can help animals exploit food more efficiently (Dyer, 1996; Van Moorter et al., 2009), maintain social dominance (Kokko et al., 2006), minimize movement costs (Stamps, 1995), reduce predation risk (Metzgar, 1967) and increase fitness (Forrester et al., 2015; Gehr et al., 2020). Despite potential benefits, animals exhibit considerable variation in their tendency to return to particular sites (Sutherland, 1998), suggesting site flexibility, as opposed to site fidelity, may be advantageous under certain conditions or in certain species. Strong site fidelity may inhibit animals from moving adaptively within their landscape and responding to changing distribution in high-quality sites (Krebs, 1971; Merkle et al., 2015; Rodenhouse et al., 1997). The possibility that site fidelity and site flexibility have fitness consequences has motivated a considerable amount of work recently aimed at quantifying variation in movement plasticity across individuals and species (Eggeman et al., 2016; Peters et al., 2019; Sawyer et al., 2019; Sutherland, 1998). An unresolved question, however, is whether an animal's strength of site fidelity is shaped by its current environment, for example due to differences in the predictability and quality of resources (van Moorter, et al., 2013; Piper, 2011; Riotte-Lambert & Matthiopoulos, 2020), or whether it is driven by an animal's strength of attraction to familiar sites, for example due to the way that spatial memory shapes movement decisions (Merkle et al., 2019). The difference between these two extremes has significant consequences for predicting how animals respond to environmental variation, including rapid landscape changes caused by humans (Bolger et al., 2008; Faille et al., 2010; Wyckoff et al., 2018).

There is considerable evidence that site fidelity is mediated by an animal's environment (Abrahms et al., 2018; Switzer, 1993). Animals clearly make adaptive movements towards resources (Krebs, 1971), and if those resources are heterogeneous in space and spatially and temporally predictable, site fidelity may emerge simply because individuals revisit high-quality sites and avoid poor quality sites (Riotte-Lambert & Matthiopoulos, 2020). One implication is that as resource quality and predictability change over time and space, animals will move to more favourable sites. In landscapes where resources are unpredictable in space, movements are expected to be more nomadic and individuals may return irregularly to particular sites (Teitelbaum & Mueller, 2019). Environmental predictability may also explain why the strength of site fidelity often appears to change seasonally. For instance, weather events can drive stochastic fluctuations in site availability at certain times of year (e.g. due to variable snow depth (Northrup et al., 2016)) and reduce the strength of site fidelity during these periods. Furthermore, familiar sites may be particularly attractive during important life-history events when site quality is strongly tied to individual fitness, such as during parturition (Fancy & Whitten, 1991), mating (Festa-Bianchet, 1986) or at nest sites (Hoover, 2003).

Other drivers of site fidelity, such as those based on memory, can reinforce the strength of site fidelity and modify how individuals respond to variation in site quality and environmental predictability (Merkle et al., 2019; Sawyer et al., 2019). Strong control for site selection and navigation can arise through genetic imprinting or cultural inheritance (Berthold et al., 1992; Jesmer et al., 2018) and be retained

through memory (Fagan et al., 2013). In some cases, the engrained or memorized control of site fidelity is so strong that it can prevent individuals from responding adaptively to environmental change (Merkle et al., 2015). For instance, Wiens et al. (1986) demonstrated that migratory birds exhibit extremely strong fidelity to breeding sites, even following the experimental reduction of site quality. Similarly, mule deer *Odocoileus hemionus* in the Western United States and moose *Alces alces* in Norway continued migrating along the same routes each year despite increasing levels of anthropogenic disturbance, presumably to the animals' detriment (Andersen, 1991; Wyckoff et al., 2018).

Site fidelity may also be strongest where an animal's long-term knowledge about local conditions at particular sites outweighs the benefits of exploring new, potentially poor, sites (Abrahms et al., 2018; Bevanda et al., 2015; Krebs, 1971; Merkle et al., 2015; Piper, 2011; Wakefield et al., 2015). In this case, the decision to revisit sites is conditional on an individual's past experiences with that site (Van Moorter et al., 2009). One possibility is that individuals maintain an attraction to familiar sites until those sites yield unsuccessful outcomes, that is, the 'win-stay, lose-switch' strategy (sensu Switzer, 1993). Under this strategy, unsuccessful outcomes in the past will cause individuals to switch to new sites during subsequent time periods. Empirical support for 'win-stay, lose-switch' as a driver of variation in site fidelity comes largely from songbirds and seabirds that return to nest sites following years with high breeding success (Hoover, 2003; Wakefield et al., 2015). Because this driver involves a conditional response to environmental variation in site quality, the strength of its effect on site fidelity can also vary seasonally with changes in site quality, as above. Furthermore, the development of preferences for familiar sites requires that individuals learn and remember spatial information (Piper, 2011). If animals use cumulative experiences to inform decisions about site selection, older individuals may also develop stronger preferences for sites because those animals have more opportunities to learn the locations of high-quality sites (the 'experience' driver; Jesmer et al., 2018; Teitelbaum et al., 2016).

In this study, we use a cross-species, multi-population approach to evaluate the role of different drivers on the relative strength of site fidelity from 1 year to the next. We focus on ungulates because their relatively long life spans and diverse movement tactics provide considerable scope for individuals to integrate site preferences into their response to environmental variation (Jesmer et al., 2018; Merkle et al., 2014, 2019). Ungulates also move at a spatial scale where environmental predictability can be conveniently quantified over time using satellite remote sensing (Merkle et al., 2016; Pettorelli et al., 2005). While site fidelity has long-interested scientists who study ungulates (Edge et al., 1985; Festa-Bianchet, 1986; Geist, 1971), the drivers of variation in this behaviour have not been thoroughly evaluated, particularly across populations and taxa. Habitat loss (Morrison & Bolger, 2014), migration barriers (Sawyer et al., 2013), altered plant phenology (Middleton et al., 2013), and overhunting (Milner-Gulland et al., 2001) threaten ungulate populations globally (Bolger et al., 2008), and site fidelity may be an important behavioural process constraining an animal's response to novel or rapidly changing environments (Abrahms et al., 2018; Faille et al., 2010; Sih et al., 2011).

If site fidelity is shaped by environmental drivers, we make two predictions: (a) that fidelity is strongest in landscapes with high environmental predictability in time and space (Figure 1), and (b) that fidelity varies seasonally—for example, growing/non-growing seasons, parturition and breeding—due to variability in site quality and site availability over time. If site fidelity is conditional on past experiences at sites, we expect that poor foraging success in 1 year (here measured by resource tracking success in the springtime) will cause weaker fidelity the following year, and more generally, that older animals will have stronger fidelity because they have greater cumulative experience to inform movement decisions (Figure 1). A definitive test of the role of past experience or memory is not possible without experimental approaches; nonetheless, if site fidelity is mainly shaped by experience or memory we would expect that individuals living in different landscapes would have similar strength of site fidelity within species.

2 | MATERIALS AND METHODS

2.1 | GPS-telemetry datasets

We investigated inter-year site fidelity using GPS-telemetry data from 8 ungulate species, 27 study sites and 669 individuals

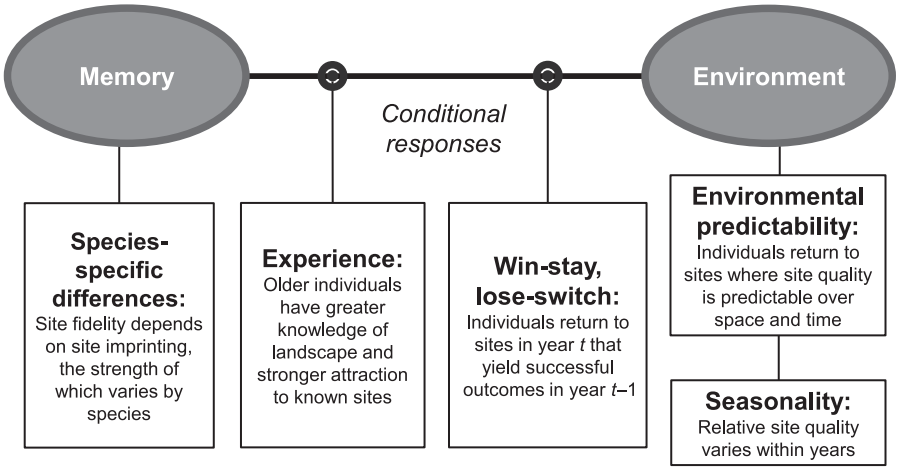

FIGURE 1 Conceptualized gradient in the drivers of site fidelity. Attraction to sites can be based on an animal's memory of the site or can simply be a response to environmental conditions at the site. Between these two extremes lies several conditional responses that depend on both knowledge from the past and environmental conditions

(see Figures S1 and S2 in Appendix S1). Species included Rocky Mountain bighorn sheep *Ovis canadensis canadensis*, Rocky Mountain elk *Cervus canadensis nelsoni*, Shiras moose *A. alces shirasi*, mule deer *O. hemionus*, pronghorn *Antilocapra americana*, barren-ground caribou *R. tarandus granti*, plains zebra *E. quagga* and white-bearded wildebeest *Connochaetes taurinus* (Table 1). Datasets of bighorn sheep, elk, moose, mule deer and pronghorn were collected in various sites in Wyoming, United States. Barren-ground caribou data were collected from the Porcupine herd in northeastern Alaska, United States and northern Yukon Territory, Canada. Wildebeest and zebra data were collected in the Serengeti-Mara Ecosystem in Tanzania and Kenya. Individuals that accessed known artificial feed grounds (namely Wyoming elk) were excluded. GPS datasets consisted of adult females that were ≥1.5 years old at the time of collar deployment. Individual-level data were collected for varying time lengths between 2001 and 2019. Due to battery-life constraints on collars, no individuals were monitored for more than 3.25 years. Animal capture and handling was performed in accordance to local regulations and protocols in the United States, Tanzania and Kenya. We performed two data pre-processing steps on these data: (a) subsample GPS datasets to daily fix rates, and (b) censor GPS data so that site fidelity was calculated up to a maximum of 1 year per individual. Thus, we did not consider whether fidelity changed across multiple years within individuals. The median data length in our study was 721 days per individual.

2.2 | Quantifying site fidelity

We defined 'sites' as the set of GPS locations visited by collared animals during the second year (year *t*) of a telemetry dataset. 'Site fidelity' was then measured as the shortest Euclidean distance between each site in year *t* and a set of sites around a corresponding window of time in year *t* − 1 (Conner & Leopold, 2001). More formally, site fidelity was the minimum inter-year distance (*IYD*) between the spatial location (*xy*) for individual *i* on Julian date *j* in year *t* and the set of spatial locations within a window of time (*w* days) surrounding the Julian date *j* during the previous year *t* − 1:

$$IYD_{i,j} = \min\left(dist\left(xy_{i,k,t-1}, xy_{i,j,t}\right)\right),$$

where:

$$j - \frac{w}{2} < k < j + \frac{w}{2}. \quad (1)$$

We were specifically interested in inter-year site fidelity because ungulates often follow spatial gradients in resources on an annual basis (i.e. an annual migration) and therefore individuals varied in their tendency to return to the same sites across years. We favoured this distance-based metric over other common indices of site fidelity (e.g. range overlap) because it provided a measure of spatial proximity on an absolute scale (km) that was more relevant to spatial conservation planning than other relative or unit-free scales (Berger, 2004). Note the strength of site fidelity was inversely related to *IYD*, such that larger *IYD* values implied weaker site fidelity.

The window of time in year *t* − 1 helped account for variation in the timing of large-scale movements between years, for example in migration timing due to differences in the phenology of green-up. We calculated a different window size for each species by estimating the start and end dates of 'migratory' and 'mixed-migratory' movements within individuals in consecutive years using models fit to net-squared displacement with the package migrateR (Spitz et al., 2017). Models were tuned to improve model fit and convergence, and individuals not exhibiting a migratory or mixed-migratory movement in consecutive years were excluded for the purpose of window size calculations. The standard deviation of start and end dates was measured across years within individuals, and mean values for each species were estimated from a linear mixed effect model, with a random effect for individual. Window sizes then corresponded to two standard deviations in this mean estimated value (Table 1). Bighorn sheep and pronghorn did not have sufficiently long datasets to estimate window sizes across multiple years, so window sizes for these species were set to the mean window size for other Wyoming species (72 days; Table 1). A sensitivity analysis across a range of window sizes (see Figures S3 and S4 in Appendix S1) suggested that *IYD* was relatively insensitive to changes in the window size, particularly for window sizes larger than those selected in the study. Moreover, our

TABLE 1 Summary of GPS collar datasets by species, ordered by mean inter-year distances (*c.f.* Figure 2)

Species	Common name	No. individuals	No. study areas	Window size in days[a]	Annual home range size median (IQR) km[a]
Odocoileus hemionus	Mule deer	167	5	44	479 (785)
Alces alces	Moose	80	3	84	79 (133)
Ovis canadensis	Bighorn sheep	58	4	72	57 (45)
Cervus elaphus	Elk	205	8	88	489 (540)
Antilocapra americana	Pronghorn	81	4	72	578 (880)
Equus quagga	Zebra	15	1	110	5,678 (1,443)
Connochaetes taurinus	Wildebeest	26	1	86	17,883 (2,513)
Rangifer tarandus	Caribou	37	1	24	97,328 (41,184)

[a]Window size represents variation in the timing of movements across years (see Section 2).

[b]Estimated by individual from 99% contour of utilization distributions using Brownian Bridge movement models.

estimated window sizes corresponded well with resources-based estimates of inter-annual variation: across all locations occupied by study animals in Wyoming between 2001 and 2015, peak green-up date in the spring varied by 84 days, based on parameters estimated by fitting logistic models to normalized difference vegetative index (NDVI) data (Bischof et al., 2012; Merkle et al., 2016).

2.3 | Seasonality

To compare the relative strength of site fidelity across seasons, we developed linear mixed models (LMMs) for each species separately and modelled time-varying *IYD*. We treated week of the year (weeks 1–52) as a dummy fixed effect variable, with *Individual* nested within 'study area' as random intercepts. We assessed weekly differences in *IYD* by evaluating overlap of 95% confidence intervals during different phenological and life-history periods of the year: green-up period, growing season, non-growing season, parturition and rut. Green-up corresponded to springtime and was delineated using NDVI time series (see '*Win-stay, lose-switch*' below; Merkle et al., 2016). Growing and non-growing seasons were defined as summer (June–August), winter (December–February) in high latitudes and late wet season (April–May) and late dry season (September–October) in the tropics. Life-history periods were delineated through a literature search (see Appendix S2).

2.4 | Environmental predictability

We decomposed environmental predictability in terms of 'constancy' and 'contingency' (Colwell, 1974; Riotte-Lambert & Matthiopoulos, 2020) using values of NDVI collected across time and space. NDVI is an indicator of photosynthetic activity and is often used in herbivore studies as a proxy for forage resource availability (Pettorelli et al., 2005). NDVI was derived from MODIS satellite imagery (product 'MOD13Q1v006') at a resolution of 250 metres per pixel and collected every 16 days from 2000 to 2019.

Spatial constancy provided a measure of the landscape's spatial homogeneity within the individual's home range, while *Temporal constancy* provided a measure of the stability over time of local NDVI, averaged over the individual's home range. Both metrics were calculated similarly using Colwell's (1974) constancy measure *C*, which was based on Shannon's (1948) entropy, *H* as:

$$C = 1 - H/\log(n),$$

where:

$$H = -\sum_{i=1}^{n} P_i \times \log\left(P_i\right). \quad (2)$$

Here, *P* is the proportion of NDVI values that fall within an interval *i*, across *n* possible NDVI intervals. *Temporal constancy* was calculated on a per-pixel basis across all NDVI scenes and then averaged over an individual's home range, and *Spatial constancy* was calculated across all pixels within an individual's home range for the NDVI scene corresponding to the nearest date in time to each GPS location. We used $n = 100$ intervals, with each interval evenly spaced between maximum and minimum NDVI for a given set. The resulting *constancy* values ranged between 0 and 1, corresponding to low and high environmental invariance respectively.

As suggested by Riotte-Lambert and Matthiopoulos (2020), to quantify the predictability of the seasonal cycling of resources, that is, *Temporal contingency*, we quantified the normalized spectral entropy of NDVI (Zaccarelli et al., 2013). Normalized spectral entropy applies the entropy measure to the power spectrum of a time series and here quantified the tendency with which NDVI values reoccurred at periodic intervals (Zaccarelli et al., 2013). To our knowledge, this is the first time that this measure has been used in movement ecology. We normalized and scaled the spectral entropy of NDVI time series for each pixel so that it ranged between 0 and 1, corresponding to no periodicity and perfect periodicity respectively. We calculated this measure of contingency for each pixel used by a focal individual. We calculated spatial and temporal constancy metrics for all species but were unable to calculate periodicity values for caribou and some Wyoming animals because of breaks in the NDVI time series caused by snow cover.

2.5 | Win-stay, lose-switch

To assess if fidelity depended on past experiences, we measured resource tracking efficiency for each individual by calculating the mean absolute difference in the number of days between when an animal occupied a pixel and the date that the pixel experienced its maximum rate of green-up in that year across all dates in the springtime of year $t - 1$ (variable *Days from peak IRG*). This approach was based on the method develop by Aikens et al. (2017) and assumed that the maximum instantaneous rate of green-up (IRG) provided the highest quality of resources in that pixel, such that larger differences between the date of maximum IRG and the date occupied by animals implied poorer resource tracking (Bischof et al., 2012; Merkle et al., 2016). While individuals may differ slightly in the timing of selection of green-up resources relative to the peak of the IRG curve, past work shows that many large herbivores select for the peak IRG during the springtime (Merkle et al., 2016). Following the methods of Merkle et al. (2016), IRG and springtime start and end dates were calculated by fitting a logistic regression to the NDVI time series in each pixel during the springtime and calculating the first derivative of the curve. Mean of the absolute value of *Days from peak IRG* for each individual was then calculated across all dates in the springtime of year $t - 1$. We limited the test of 'win-stay, lose-switch' to datasets from Wyoming (bighorn sheep, mule deer, elk, moose and pronghorn) because we had difficulty fitting phenological models to data elsewhere due to aseasonality in the tropics and snow cover in the early springtime in Alaska and Canada.

2.6 | Experience

Due to the relatively short life spans of GPS collars, we assessed the relationship between age (variable *Age*) and site fidelity using a cross-sectional approach (i.e. monitoring many individuals of different ages for multiple years). We included all individuals for which ages had been estimated using rigorous ageing techniques ($n = 197$), which only included elk, mule deer, moose and pronghorn. Age at the time of capture was estimated by counting cementum annuli on a single tooth (either a vestigial canine or lower incisor) extracted at the time of capture, then sectioned and counted using standardized methods (Matson's Laboratory).

2.7 | Modelling approach

We developed a single pre-specified LMM to test each driver of site fidelity, as missing data led to different subsets of data for each driver (package 'LMER' in program R; R Core Team, 2012). We treated 'individual' as the unit of observation in all models except *Seasonality* (see above) and, prior to fitting models, calculated the mean values of all response and explanatory variables within individuals. *IYD*, *Temporal constancy*, *Spatial constancy* and *Temporal contingency* were calculated across all dates within an individual's trajectory, while *Days from peak IRG* was calculated across all springtime dates in year $t - 1$. The response variable in all models, *IYD*, was transformed prior to analysis using the natural log to meet assumptions of normality. All models except *Seasonality* included *Species* and the interaction between *Species* and the main explanatory variable of interest as fixed effects. We also developed a *Species*-only model that was used for prediction of relative species-level effects. Finally, we used a type II analysis of variance to understand whether *IYD* differed across 'study area' within *Species*, after controlling for home range size.

We included several additional variables to account for variation in *IYD* across species and datasets. First, we expected that *IYD* would increase positively with the size of the home range used by each individual because individuals moving over larger areas had access to a greater number of available sites. We controlled for this effect by including area of occurrence for each individual (i.e. *Home range*) as a fixed effect in all models. *Home range* was estimated by fitting Brownian Bridge movement models to daily relocations in the first year of data and identifying the 99% contour of the resulting utilization distribution (Horne et al., 2007). *Home range* was log-transformed prior to model fitting to improve the distribution of residuals. Second, GPS collar data came from a variety of past studies, and we assumed that individuals within studies were more ecologically and phylogenetically similar to one another than individuals in other studies due to a variety of unmeasured reasons (e.g. similar predation risk, local adaptations, learning; Jesmer et al., 2018). We therefore accounted for this variation by including 'study area' as random intercept in all LMMs (Table 1).

3 | RESULTS

Minimum inter-year distances (*IYD*) varied considerably across species (Figure 2). After accounting for the strong positive effect of *Home range* size on *IYD* (Table 2), mule deer, moose, and bighorn sheep had relatively low *IYD* (i.e. strong site fidelity), followed by elk and pronghorn (Figure 2). Zebra, wildebeest and caribou all had comparatively high *IYD* (Figure 2). In mule deer, for instance, the median *IYD* (untransformed) across all individuals was only 0.17 km (IQR: 0.12–0.26 km), implying that, despite their relatively large annual range sizes (Table 1), mule deer returned for the entire year t to within 170 metres of sites visited in year $t - 1$. In contrast, in caribou the median *IYD* was 104.5 km (IQR: 75.3–190.8 km) across individuals. *IYD* across 'study areas' differed in bighorn sheep ($F_{3,54} = 3.94$, $p = 0.01$), elk ($F_{7,197} = 2.44$, $p = 0.02$), mule deer ($F_{4,147} = 2.52$, $p = 0.04$) but not in moose ($F_{2,77} = 1.45$, $p = 0.24$) nor pronghorn ($F_{3,59} = 1.27$, $p = 0.29$). Caribou, wildebeest and zebra did not have multiple 'study areas' so inter-study differences could not be compared.

Seasonal patterns of *IYD* varied across species (Figure 3). Mule deer, moose, elk and pronghorn had relatively low *IYD* (i.e. stronger site fidelity) during the late growing season (i.e. July and August) and relatively high *IYD* during the late non-growing season (i.e. February and March). Caribou had the greatest absolute change in strength of site fidelity across seasons of any species, with low *IYD* around the parturition period (June; median *IYD* 8.5 km) and relatively high *IYD* immediately prior to the green-up period (April–May; median *IYD* 220 km). Elk similarly showed a distinct seasonal change in *IYD* between the late summer (median *IYD* 0.37 km) and mid-winter (median *IYD* 1.79 km). Bighorn sheep, wildebeest and zebra showed no discernible seasonal pattern of *IYD* (Figure 3).

Environmental predictability was an important driver of *IYD* across the eight ungulate species. The relationship between

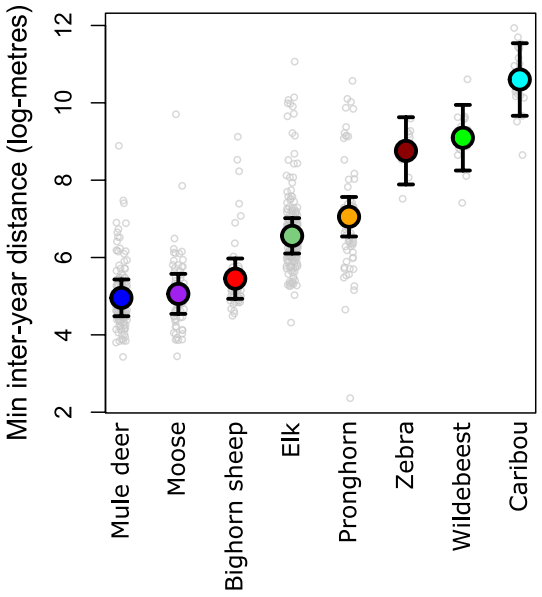

FIGURE 2 Predicted minimum inter-year distances (*IYD*) across eight ungulate species, after accounting for annual home range size. Grey circles indicate mean *IYD* of individuals across all locations

TABLE 2 Summary of coefficient estimates (β) and standard errors (*SE*) from linear mixed models of inter-year site fidelity. Bold indicates 95% confidence intervals of β do not overlap zero (*c.f.* Figure 4). *Species* and interaction effects were relative to bighorn sheep, except *Age* which was relative to pronghorn

	1. Temporal constancy		2. Spatial constancy		3. Temporal contingency		4. Days from peak IRG		5. Age	
Model	β	*SE*	β	*SE*	β	*SE*	β	*SE*	β	*SE*
Focal variable										
(Intercept)	**3.51**	**1.15**	**5.08**	**0.53**	**6.97**	**0.98**	**4.07**	**0.90**	**4.81**	**0.72**
Constancy time	1.68	3.82								
Constancy space			**−10.01**	**4.18**						
Periodicity					**−5.06**	**1.74**				
Days from peak IRG							−0.03	0.02		
Age									−0.06	0.09
Species										
Caribou	4.60	2.84	**3.53**	**4.09**						
Elk	0.81	1.28	−0.84	0.57	−0.97	1.57	−2.63	1.19	−1.07	0.57
Mule deer	−0.32	1.23	**−1.62**	**0.57**	−1.71	1.90	−0.91	1.35	−1.06	0.52
Moose	−0.82	1.54	**−1.79**	**0.66**	−1.36	3.18	−1.48	1.17	−1.72	0.62
Pronghorn	0.07	1.46	0.65	0.75	−0.95	21.09	0.88	1.34		
Wildebeest	4.04	2.55	**3.64**	**2.15**	3.00	2.26				
Zebra	0.71	7.29	0.28	1.28	−5.10	7.43				
Focal:species interactions										
Focal variable: caribou	−4.33	12.51	1.76	9.93						
Focal variable: elk	−1.40	4.32	**11.52**	**4.75**	3.00	2.67	0.10	0.04		
Focal variable: mule deer	0.18	4.04	**12.30**	**4.54**	3.19	3.02	**0.06**	**0.05**		
Focal variable: moose	2.78	6.24	**13.33**	**5.38**	2.64	4.93	0.04	0.04		
Focal variable: pronghorn	1.40	4.34	6.54	4.77	3.00	32.51	−0.02	0.06		
Focal variable: wildebeest	−14.05	14.21	−11.28	18.17	−5.23	5.55				
Focal variable: zebra	4.33	48.37	9.14	8.86	15.88	21.08				
Home range (log-km)	**0.41**	**0.06**	**0.40**	**0.06**	**0.34**	**0.08**	**0.61**	**0.11**	**0.43**	**0.11**
Random effects										
Population	0.26		0.32		0.38		0.83		0.19	
Residual	0.87		0.86		0.82		1.00		0.82	

Spatial constancy and *IYD* varied by species (Figure 4a; Table 2). As *Spatial constancy* increased (i.e., greater invariance in NDVI within home ranges), *IYD* increased in elk, moose, mule deer and caribou, but decreased in bighorn sheep, pronghorn, wildebeest and zebra (Figure 4a). In contrast, *Temporal constancy* (i.e. invariance in NDVI across time) was unrelated to *IYD*, with no detectable interactions between species and *Temporal constancy* (Table 2). *Temporal contingency* (i.e. regularity of NDVI cycles across time) was negatively related to *IYD*, with no detectable effect of the interaction between species and *Temporal contingency* on *IYD*, suggesting site fidelity was stronger in areas with greater periodicity in NDVI regardless of species (Figure 4b; Table 2). *Temporal contingency* was relatively low in areas visited by wildebeest ($M \pm SE$: 0.373 ± 0.007) and zebra (0.351 ± 0.003), and relatively high in areas visited by moose (0.661 ± 0.003) and mule deer (0.660 ± 0.003).

Elk were the only species to exhibit the 'win-stay lose-switch' strategy in which the success of greenness tracking in the springtime

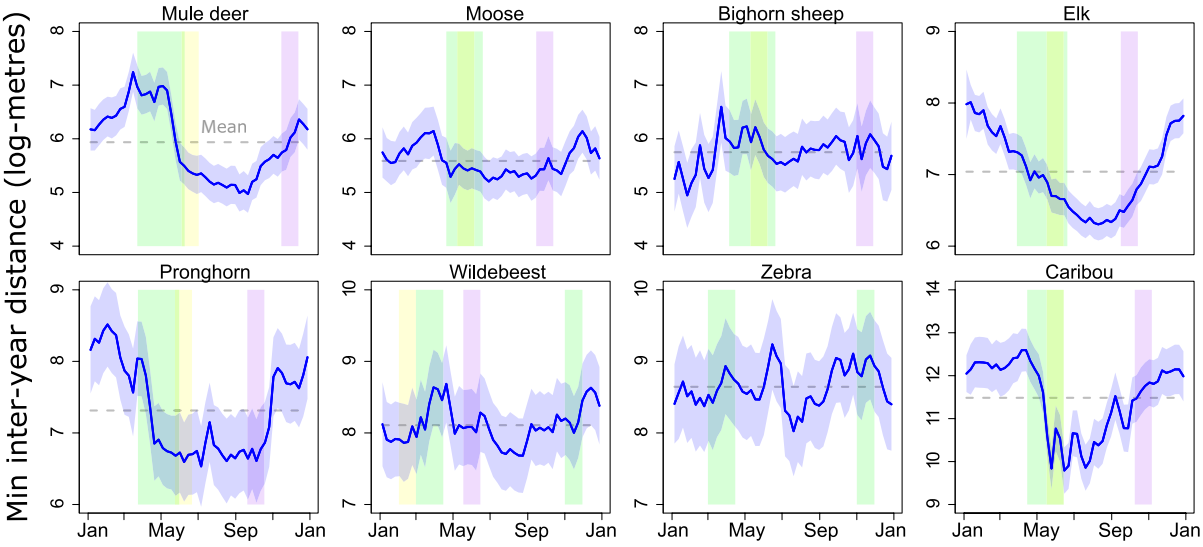

FIGURE 3 Predicted seasonal patterns of minimum inter-year distances (*IYD*, mean and 95% CI) across species. Larger *IYD* values imply weaker site fidelity. Vertical green bars denote the green-up period, that is, spring in high latitude areas and early wet season in the tropics, vertical orange bars denote parturition and vertical purple bars denote rutting, by species. Parturition and rut dates were identified in literature (see Appendix S2). Zebra are asynchronous breeders, so lack clear parturition and breeding periods. Predictions do not account for home range size because data were modelled with individuals as random intercepts

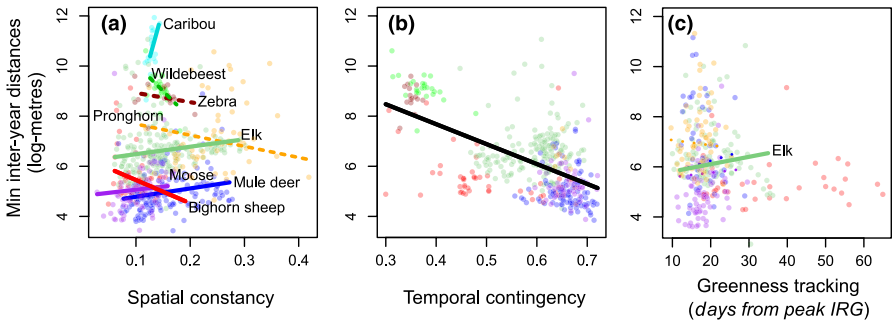

FIGURE 4 Predicted effects of (a) spatial constancy, (b) temporal contingency and (c) greenness tracking (days from peak IRG) on minimum inter-year distances (*IYD*) between years $t-1$ and t among individual ungulates. Solid coloured lines indicate species interactions that were different from the reference level, bighorn sheep (*c.f.* Table 2). Black line indicates the mean overall effect of temporal contingency on *IYD*. Lower *IYD* values (*y*-axis) imply stronger inter-year site fidelity

(i.e. *Days from peak IRG*) in year $t-1$ was positively related to spring-time *IYD* in year t (Figure 4c; Table 2). However, the relationship between *Days from peak IRG* and *IYD* in elk was not detected in other window sizes (Appendix S1), suggesting the pattern was not as robust as other focal variables. Bighorn sheep, moose, mule deer and pronghorn showed no effect of *Days from peak IRG* on *IYD*. We also found no relationship between animal *Age* and *IYD* in any of the species with available age data (Table 2; age ranges (sample size): mule deer 2–12 years old ($n = 167$); elk 3–17 years old ($n = 205$); pronghorn 2–8 years old ($n = 81$); moose 2–13 years old ($n = 80$)).

4 | DISCUSSION

Despite their long-distance movements and complex patterns of dispersion at the population level, ungulates often have a strong tendency to revisit sites across years at the individual level (Cameron et al., 1986; Edge et al., 1985; Merkle et al., 2015; Morrison & Bolger, 2012; White et al., 2007; Wittmer et al., 2006). Yet, comparisons across populations and species are rare, making it difficult to evaluate whether 'strong' or 'weak' site fidelity reported from one study implies an equivalent intensity elsewhere. A formidable challenge in this regard is to determine whether observed patterns of site fidelity are driven by an animal's environment, or by factors such as those controlled by memory. By examining patterns of site fidelity across a range of species, populations and landscapes, and by accounting for variation in home range size across individuals, our study demonstrates that environmental factors, such as environmental predictability and seasonality, are important drivers of inter-year site fidelity in ungulates. Relatively strong site fidelity observed in some species (Figure 2) raises the possibility that an animal's response to the environment may interact with drivers such as experience or memory to determine the spatial proximity with which the animal returns to particular sites each year.

A key finding was that site fidelity was related to components of environmental predictability. The effect of spatial constancy, that is, the degree of spatial homogeneity of the landscape within an individual's home range, depended on species. Switzer (1993) suggested that when resource variability is low across space, switching to new sites offers limited foraging benefits yet may require higher travel costs, so site fidelity should remain relatively strong. Bighorn sheep, for example, exhibited a strong negative relationship between *IYD* and spatial constancy, suggesting stronger site fidelity in more homogenous landscapes, which may be related to high travel costs of moving between suitable sites in mountainous terrain. Yet, in other species (caribou, elk, moose and mule deer) site fidelity was weaker in more spatially homogenous landscapes (Figure 4a). This pattern appears consistent with other ungulates, such as Mongolian gazelle, whose nomadic movements across years appear linked to low spatial predictability in vegetative greenness (Mueller et al., 2008).

For all species, site fidelity was strongest in areas with high periodicity in NDVI (i.e. temporal contingency) but was unrelated to homogeneity in NDVI over time (i.e. temporal constancy), suggesting that predictability in the annual timing of vegetative greening and browning is more important than the magnitude of variability. Broadly speaking, temporal contingency should correlate with latitude because seasonality increases towards the poles (Mueller et al., 2011; Peters et al., 2019). Indeed, the highest values occurred in the home ranges of temperate species while the lowest temporal contingency values occurred in the home ranges of tropical species (wildebeest and zebra; Figure 4). This suggests that both within and between species, site fidelity across years may be stronger at higher latitudes and in home ranges influenced by greater seasonality, all else being equal. Peters et al. (2019) showed that migratory propensity (i.e. the proportion of a population that migrates) in roe and red deer increased in more landscapes with greater contingency and spatial heterogeneity across a latitudinal gradient in Europe, demonstrating how environmental predictability can modulate the regularity of movements in large herbivores.

Variation in site fidelity across seasons provides further support for the hypothesis that site fidelity is driven by environmental factors. Overall, site fidelity was strongest during the late summer, weakest during the late winter, and invariant across the year in tropical species (wildebeest and zebra) and in bighorn sheep (Figure 3). We interpret seasonal variation in higher latitude areas as being driven by an attraction to localized patches of high-quality forage during the summer, and a variable response to stochastically available snow-free foraging and shelter sites during the winter (Northrup et al., 2016). Caribou exhibited their strongest site fidelity during the parturition period, highlighting the importance of calving sites to caribou which has been found previously (Faille et al., 2010; Fancy & Whitten, 1991). Caribou also had the most dispersive patterns of inter-year movements, with annual home ranges that were orders of magnitude larger than other study species (Table 2). High spatiotemporal variability in the patterns of spring snowmelt, green-up and forage abundance across the annual range of the Porcupine caribou herd has caused large distributional shifts in caribou concentrations from year to year (Griffith et al., 2002), including an eastward shift of the winter range into Canada during the 2000s and a more recent shift westward. Thus, in caribou, the need to search across vast distances and to exploit variation in snow, ice and forage availability appear to outweigh the benefits of returning to familiar locations, except, to some extent, during parturition.

Elk were the only species to modify inter-year movements based on their success in greenness tracking the previous spring, suggesting these animals employ a 'win-stay, lose-switch' strategy. Elk exhibited relatively weak site fidelity overall, but strong site fidelity in the spring and summer, suggesting this tactic may enable additional flexibility in the springtime to tune movements with green-up phenology (Merkle et al., 2016). We found no evidence that individual age/experience modifies the strength of site fidelity in adult ungulates, despite a relatively large sample size ($n = 196$) of individuals that encompassed a range of estimated ages (1.5–20.5 years old). One possibility is that learning of sites occurs largely during the first several years of life, before collars were deployed in this study, and that subsequently the strength of attraction for known sites does not change over the lifetime of adult ungulates (Nelson & Mech, 1999; Sawyer, LeBeau, et al., 2019; Sweanor & Sandegren, 1988). More conclusive evidence for such age effects, however, requires longitudinal tracking of individuals over the course of lifetimes, or even generations (Fagan et al., 2013).

Large unexplained differences in site fidelity observed among species may reflect variation in attraction to previously visited sites that arise either through memory or genetic encoding (Riotte-Lambert & Matthiopolous, 2020). In bighorn sheep, mule deer and elk species, however, site fidelity varied across different study areas, which would not be expected if the primary driver of species-level variation was an attraction to previously visited sites. Other unmeasured factors may also generate these observed differences. For instance, avoidance of areas previously visited may help large herbivores evade predators through a 'shell game' (Gehr et al., 2020; Mitchell & Lima, 2002), or it may reduce exposure to sites contaminated with long-lived pathogens, which may be particularly relevant in species that form dense aggregations, such as wildebeest and caribou. Our study also did not consider density-mediated effects because reliable abundance/density estimates were unavailable in many populations. The effect of density on ungulate migration tactics (Eggeman et al., 2016; Sweanor & Sandegren, 1989) and habitat selection (Van Beest et al., 2013) has been noted elsewhere, and if site fidelity is density-dependent, we would expect its effect to be most apparent during the non-growing season when density modulates per capita forage availability (Mduma et al., 1999).

5 | CONCLUSIONS

Widespread environmental change requires an understanding of how animals modify movements and space use to accommodate changes in habitat or barriers to movement (Sawyer et al., 2013). Behavioural constraints such as site fidelity can limit the ability

of individuals to select the highest quality habitats within a landscape (Merkle et al., 2015), and these constraints can be detrimental if behaviours persist in spite of decreasing benefits in the face of rapid environmental change (Sih et al., 2011). Our study demonstrates that site fidelity is associated with a number of environmental drivers and that, at least in elk, site fidelity is conditional on experiences at sites in the previous year, suggesting that ungulates are equipped with some flexibility to respond spatially to environmental change (Riotte-Lambert & Matthiopoulos, 2020). Nonetheless, a number of studies have observed animals returning to sites even after changes to their environment (Wiens et al., 1986; Wyckoff et al., 2018), suggesting that their attraction to known sites overrides responses to their environment, at least in the short term. For species with weak fidelity, there is a need to conserve landscapes in ways that ensure animals retain access to large areas that contain ephemeral resources that can vary substantially in space from year to year (Nandintsetseg et al., 2019; Teitelbaum & Mueller, 2019). Future studies that quantify behavioural flexibility across lifetimes of individuals and that experimentally manipulate key resources would allow insight into the magnitude and relative strength of environmental and memory effects (Van Moorter et al., 2013).

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AUTHORS' CONTRIBUTIONS

T.A.M., J.A.M. and M.J.K. conceived the study; T.A.M., J.A.M. and E.O.A. performed analyses with input from M.J.K., J.G.C.H. and L.R.-L.; Data were collected by J.G.C.H., J.L.B., R.B.B., A.B.C., S.P.D., W.S.F., B.G., A.D.M., K.L.M., B.O., H.S., K.T.S., J.A.S., K.L.T. and M.J.K.; T.A.M. led the drafting of the manuscript, and all authors contributed critically to the manuscript and approved it for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.31zcrjdjr (Morrison et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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