ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Divergent predator activity muddies the dynamic landscape of fear

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Funding information
East Foundation, Grant/Award Number:
PA013

Handling Editor: Bryan Kluever

Abstract

The landscape of fear (LOF) hypothesis is a unifying idea explaining the effects of predators on the space use of their prey. However, empirical evidence for this hypothesis is mixed. Recent work suggests that the LOF is dynamic, depending on the daily activity of predators, which allows prey to utilize risky places during predator down times. While this notion clarifies some discrepancies between predictions and observations, support for a dynamic LOF remains mixed. The underlying assumption of a dynamic LOF is strong predictability in predator activity cycles. Work in multi-predator systems demonstrates the effect of differential behavior between predator species on the predictions of prey space use. However, none have considered the effect of intraspecific variation in predator behavior. Most, if not all, dynamic LOF studies base inference on the species-level average activity pattern, implicitly assuming similarity within the predator population. We examined the dynamics and intraspecific variation in activity cycles within a population of coyotes (*Canis latrans*). We found seasonality in the predictability of coyote behavior, as well as divergent nocturnal and crepuscular activity patterns between individuals during summer. Activity dynamics were not related to range size, sex, body mass, or habitat complexity, but did vary by year. These results suggest that the predictability of activity patterns is seasonally dynamic, and failure to account for intraspecific variation in activity may cloud inference in LOF studies. We argue that future studies should not neglect the potential complexity of predator behavior with simplistic assumptions. By considering intraspecific variation in activity patterns, we may gain a clear picture of LOF dynamics.

KEYWORDS
activity cycles, autocorrelation, *Canis latrans*, coyote, functional data analysis, GPS telemetry, movement

INTRODUCTION

The landscape of fear (LOF; Laundre et al., 2001) hypothesis states that prey species perceive spatial variation in predation risk and navigate this landscape to balance foraging requirements and risk. This phenomenon is thought to underlie behaviorally mediated trophic cascades (Bliecher, 2017), and explain nonconsumptive

effects of predators on prey species (Preisser et al., 2005). However, empirical evidence of LOFs has been mixed in the literature (Palmer et al., 2017). Recent work suggests that this landscape is dynamic at multiple timescales, and is influenced by the activity patterns of predators (Kohl et al., 2018; Palmer et al., 2017). Because of this dynamism, spatial segregation of predators and prey changes through time, masking LOF predictions if time was not considered. Thus, predator diel cycles are linked to trophic cascades, and may have far-reaching impacts on communities and ecosystems (Bliecher, 2017).

The underlying assumption of a dynamic LOF is strong predictability of predator cycles (Dodson, 1990; Smith et al., 2019). Behavioral differences among predator species in multi-predator systems can impact the predictability of predation risk (Schmidt & Kuijper, 2015). For example, Morosinotto et al. (2010) observed differential behavioral responses of pied flycatchers (*Ficedula hypoleuca*) to two superficially similar species of owl (family: Strigidae) with different activity patterns. One would not accurately predict prey response by considering only one predator behavior. We posit that the same may be true of different behaviors across individuals within a predator species.

Most studies of the temporal dynamics of a LOF implicitly assume that cycles in activity, such as nocturnal or crepuscular behavior, are similar across individuals within predator populations (Eriksen et al., 2011; Palmer et al., 2017). However, this may not be true for many species (Kohl et al., 2018; Smith et al., 2019). Many predators exhibit dietary and behavioral plasticity across individuals, which contributes to the broad distribution of many species (Slayter et al., 2013). Although some LOF studies consider behavioral variation of a predator species across regions (e.g., Yang et al., 2018), variation among individuals within a local population has not been considered. Predators within a population can vary daily activity cycles to reduce both inter- and intraspecific competition (Alanara et al., 2001; Lucherini et al., 2009), which are in turn linked to foraging strategies (Polansky et al., 2013). Thus, not all individuals within a predator population necessarily represent the same risk to a given prey species.

Prey species may perceive differences in risk between individual predators directly, or by recognizing spatio-temporal variation in risk of predation events rather than the risk of encountering predators per se (Lank & Ydenberg, 2003; Palmer et al., 2017). Ungulates appear able to distinguish differences in risk posed by predators of the same species (Gese, 1998). If indeed prey can distinguish threatening from nonthreatening predators, regardless of the mechanism, the activity cycles *of threatening predators* are of interest. If the behaviors of

threatening individuals manifest in different activity cycles than those nonthreatening ones, the overall pattern of the predator species will reflect a combination of distinct, component behaviors. Failing to account for these differences will bias parameter estimates, and add unmodeled statistical noise to analyses. Thus, inference into the effects of predator activity on their prey may be confounded by differential behavior, foraging, and perceived threat to prey among predators in the same population. Ignoring this variation could cloud inference in LOF settings but is difficult to address, given the small sample sizes and capture biases typical of carnivore studies (Kohl et al., 2018; Thompson et al., 2012). Researchers need information on the dynamics of the activity cycles of individuals in order to explicitly account for their effects, or control for them in study designs.

As a model, we examined the degree and nature of behavioral variation within a population of a generalist carnivore: the coyote (*Canis latrans*). Coyotes are a ubiquitous species in North America that exhibits a great deal of behavioral variation (Bekoff & Gese, 2003; Bekoff & Wells, 1986). Their wide range and generalist, predatory habits have led to many conservation and management issues—ranging from impacts on endangered species through predation (Boisjoly et al., 2010) or hybridization (Hinton et al., 2018), to agricultural impacts on crops (Holzman et al., 1992) and livestock (Sacks & Neale, 2007), to the spread of zoonotic diseases (Way & White, 2013). Despite the numerous issues associated with coyotes, and the importance of animal behavior in effective conservation and management (Berger-Tal et al., 2011), factors affecting coyote activity cycles are poorly understood.

Few studies examine individual variation in coyote activity cycles, but scientists recognize some tendencies. For example, coyotes tend to exhibit nocturnal (Holzman et al., 1992) or crepuscular behavior (Andelt, 1985; Arias-Del Razo et al., 2011; Gipson & Sealander, 1972; Woodruff & Keller, 1982). If individual coyotes choose between alternative activity strategies, researchers will need reliable predictors to differentiate individuals exhibiting similar patterns. Which strategy an individual adopts may depend on straightforward predictors, such as sex, habitat characteristics, or resident status. Male and female activity patterns may diverge during the breeding season, when females are thought to exhibit less evening activity than males (Andelt, 1985; Way et al., 2004). This relationship could potentially guide the timing of sex-targeted management actions to reach conservation goals. Coyotes may also adapt their hunting strategies to the structure of their habitats, where the success of a particular hunting strategy will depend on vegetation density and visibility (Arias-Del Razo et al., 2012;

Thibault & Ouellet, 2005; Ward et al., 2019). Thus, vegetation density may be linked to activity cycles (Kitchen et al., 2000), and could be manipulated to achieve conservation goals. Finally, Andelt (1985) reported limited evidence that diel activity cycles varied by territorial residency status, which manifests in individual range sizes (Kamler & Gipson, 2000) and may be related to body mass (Bekoff & Wells, 1986). Lethal management efforts disproportionately target nonresident coyotes (Sacks et al., 1999), which may bias them toward a particular activity pattern if this relationship holds. Because of this, range size and body mass may be indicative of a relationship between residency status and activity.

We examined variation in the dynamics of coyote activity patterns within an unharvested coyote population in southern Texas. We quantified activity cycles through time to examine seasonal trends and interindividual variation in activity dynamics. We then checked for evidence of multiple, simultaneous patterns of activity dynamics, which would undermine the appropriateness of population-level activity patterns for LOF studies. We then related their variation to simple predictors to determine whether they could serve as reliable indicators of activity dynamics. Finally, we evaluated the implications of our results for inference in LOF dynamics.

METHODS

Study area

This study was conducted on the East Foundation's San Antonio Viejo Ranch (SAVR), approximately 61,000 ha of Jim Hogg and Starr counties in southern Texas (Latitude: 26.9557321, Longitude: −98.8335374; Figure 1). The East Foundation's ranches are managed as a living laboratory to promote the advancement of land stewardship through ranching, science, and education. The area is dominated by shrub savannas, primarily composed of honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), cat-claw acacia (*Acacia greggii*), blackbrush (*Acacia rigidula*), whitebrush (*Aloysia gratissima*), and granjeño (*Celtis pallida*), with early to mid-successional grasses, including three-awns (*Aristida* spp.), little bluestem (*Schizachyrium scoparium*), and windmill grasses (*Chloris* spp.). Lethal harvest and harassment of native animals, including coyotes, has not occurred on SAVR since the East Foundation's inception in 2007. Further, coyotes were only harvested occasionally on the ranch over its recorded history, and there were no substantive lethal management efforts between 1915 and 2007. This region persistently features high coyote densities (Andelt, 1985; Bekoff & Gese, 2003; Knowlton, 1972; Windberg, 1995). These characteristics provide a unique opportunity to study activity dynamics in an unharassed, saturated coyote population.

Coyote capture and telemetry

We captured a total of 40 coyotes across three capture events by helicopter using a net gun (Gese et al., 1987). Captures occurred on 10 December 2016 ($n = 10$) and 1 April 2017 ($n = 6$), and 25–26 January 2018 ($n = 24$). We fitted each coyote with a Vertex Plus or Vertex Lite satellite GPS collar (Vectronic Aerospace GmbH, Berlin), and released it at the site of capture. Collars deployed in 2016–2017 were programmed to release from the animal on 1 January 2018, while those deployed in 2018 were programmed to release on 31 January 2019. These collars were programmed to collect location data every 1 ($n = 24$) or 2 ($n = 16$) hours. We filtered hourly data to 2-h intervals to standardize across all collars. Three coyotes died within 3 months of their respective capture dates and were excluded from these analyses. An additional four collars failed over the course of the study, leaving $n = 31$ coyotes considered in this study. We collected an average of 4189 locations per coyote (SD = 465) during the study period.

Statistical analyses

Except where indicated, all analyses were performed in R (R Core Team, 2017). We estimated individual range size as the area of the 75% isopleth of a fixed kernel density estimate of each individual's utilization distribution (Worton, 1989) using the *adehabitatHR* package (Calenge et al., 2009).

We estimated percent canopy cover within coyote ranges based on 1-m resolution National Agricultural Imagery Program imagery from 2016 (https://tnris.org/; accessed 24 April 2017). These images were merged and color matched in ArcGIS 10.4 (ESRI, Redlands, CA). Pixels were classified as woody canopy cover or noncover using an interactive supervised classification (Campbell & Wynne, 2011). We used a roving window to calculate percent canopy cover at 10-m resolution. We calculated the average canopy cover within each coyotes' range using zonal statistics tools in the spatial analyst toolbox, within ArcGIS.

We converted each series of locations to a trajectory of movement vectors, defined in terms of step lengths and turning angles, using the *adehabitatLT* package (Calenge et al., 2009). Since locations were collected on a
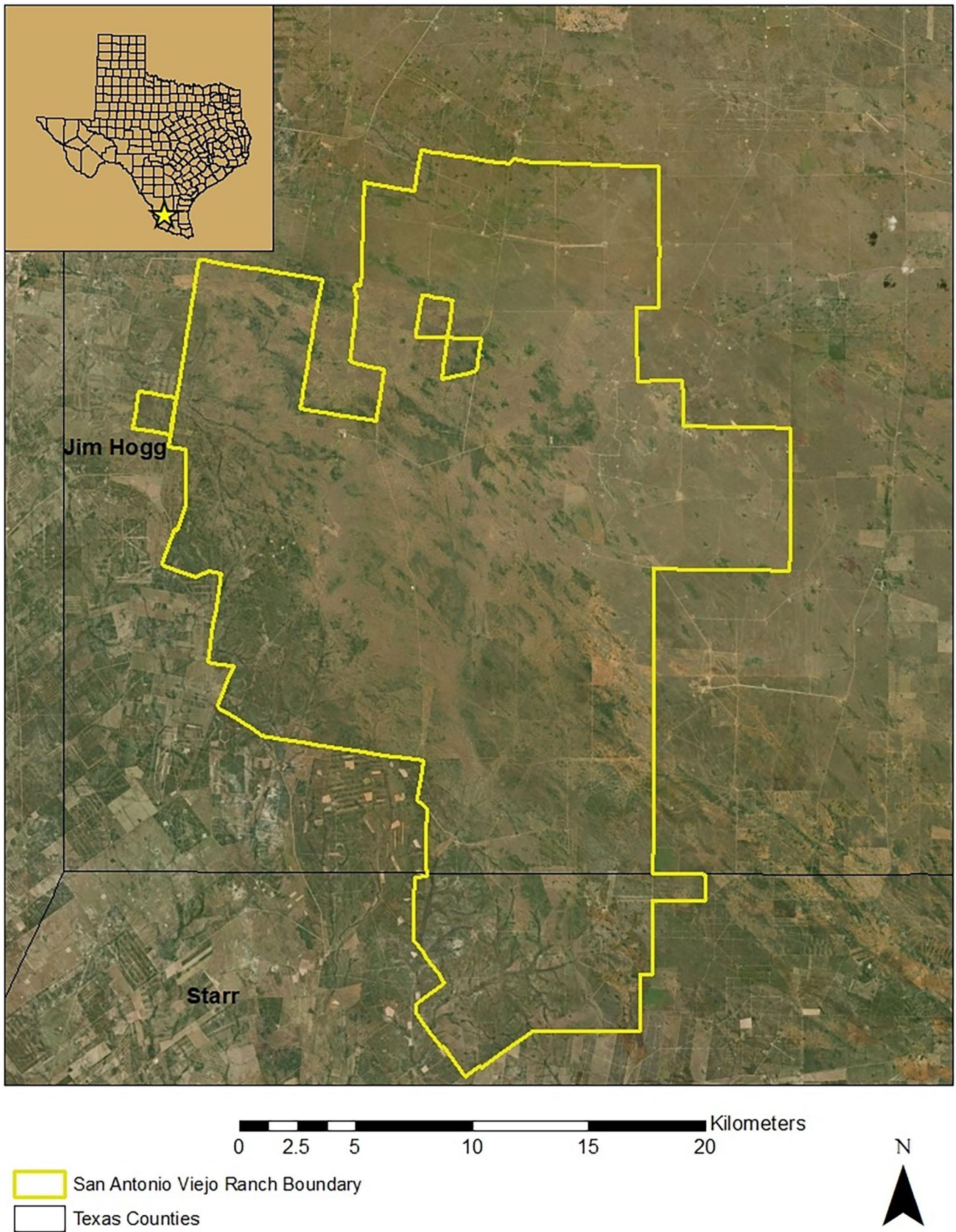
FIGURE 1   Map showing the location of the San Antonio Viejo Ranch, in Jim Hogg and Starr counties of southern Texas

regular time interval, we took the sequence of step lengths as a measure of net movement activity through time (Turchin, 1998). Missing values resulting from missed GPS fixes were interpolated using the weighted moving average procedure implemented in the *imputeTS* package (Moritz & Bartz-Beielstein, 2017). The average fix success rate was 0.98 (SD = 0.015), thus any effects of missed fixes or the interpolation of the step length series were assumed to be negligible.

We adapted the analytic approach of Cushman et al. (2005) for the analysis of nonstationary animal activity patterns. They used a roving window approach to examine changes in autocorrelation of elephant space use, capturing complex changes in behavior through time. We applied a similar roving window to capture changes in temporal autocorrelation in coyote velocity. Patterns in autocorrelation reveal hidden periodicities in time series, and allow visual differentiation of patterns, such as crepuscular and daily behavior cycles, including nocturnal and diurnal behavior (Boyce et al., 2010). We used 15-day, non-overlapping windows beginning on 10 December and advancing by 15 days until 31 January of each collar year. We chose a 15-day window in order to ensure adequate estimates of the function over enough lags to show any meaningful periodicities within the window. This relaxes the assumption of stationary autocorrelation to *local* stationarity, allowing us to capture changes in activity cycles over the course of the series. We estimated an autocorrelation function for each individual over 50 lags (100 h, using 180 steps/window) within each window as

$$\rho_\tau = \frac{\frac{1}{n}\sum \left(X_{t-\tau} - \overline{X}\right)\left(X_t - \overline{X}\right)}{S_0}, \qquad (1)$$

where ρ_τ is autocorrelation at lag τ, X_t is the value of the time series of coyote velocity at time t, $\overline{X}$ is the mean of coyote velocity time series, and S_0 is the variance of the series (Venables & Ripley, 2002). The result is an autocorrelation surface (ACS) with lags on the *x*-axis, the window sequence on the *y*-axis, and autocorrelation on the *z*-axis. The surface is interpretable visually, with variation on the *x*-axis reflecting the periodicities in activity cycles (sensu Boyce et al., 2010) and variation along the *y*-axis representing changes in activity cycles through time. By using a 15-day window, the surface captures variation in activity patterns continuously over the monitoring period, permitting interpretation of seasonal patterns without the information loss that results from assuming discrete seasons. More subtly, by evaluating autocorrelation over 50 lags (100 h), we are able to detect dampening in autocorrelation at longer lags, which indicates the changing behavior over the course of the window (Boyce et al., 2010). This combination of window length and multi-day lag intervals allows the researcher to detect behavioral changes at multiple temporal scales simultaneously. More generally, the ACS is a bivariate function representing the maximal amount of information about the individual's activity patterns, and serves as the sample unit in further analysis (Ramsay & Silverman, 2002).

We took the mean and standard deviation at corresponding cells across all surfaces to produce a mean and standard deviation surface, respectively. These are analogous to the mean and standard deviation of numeric data, but cannot be reduced to a single value and are represented graphically. The mean surface represents the population-level trend in coyote behavior dynamics while the standard deviation surface identifies the regions of the surface that are most variable across individuals.

Next we centered the ACS of each coyote by subtracting the mean surface from each. We then calculated the cell-wise L^2 Minkowski distance between centered surfaces (equivalent to Euclidean distance; Montero & Vilar, 2014) to produce a $n \times n$ distance matrix. We checked for behavioral clusters with complete linkage clustering (Lance & Williams, 1967). This method is robust to noise and produces maximally linked clusters with clear discontinuities (Legendre & Legendre, 1998). We then used permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) to assess whether overall similarity in coyote behavior dynamics could be explained by sex, initial body mass, range size, brush canopy cover within ranges, or year with the *vegan* package (Oksanen et al., 2019). A summary of individual coyotes and their associated covariates is included in Appendix S1: Table S1.

RESULTS

Box plots of step lengths by hour of day revealed a pronounced lull in activity in the afternoon, thus we consider daily periodicity in activity to represent nocturnal behavior for all coyotes (Figure 2).

The mean ACS showed pronounced peaks in autocorrelation at daily lag intervals (multiples of 12), corresponding to a strong daily cycle in movements (Figure 3). The overall magnitude of autocorrelation was largest in the summer, meaning this was when coyote activity was most strongly cyclic. Autocorrelation was weak in the winter, indicating weakly cyclic or acyclic activity patterns. This suggests that temporal variation in coyote activity is least predictable by prey in winter. The standard deviation surface revealed that the majority of variation in autocorrelation was at crepuscular intervals from mid-April through July, punctuated by a lull in
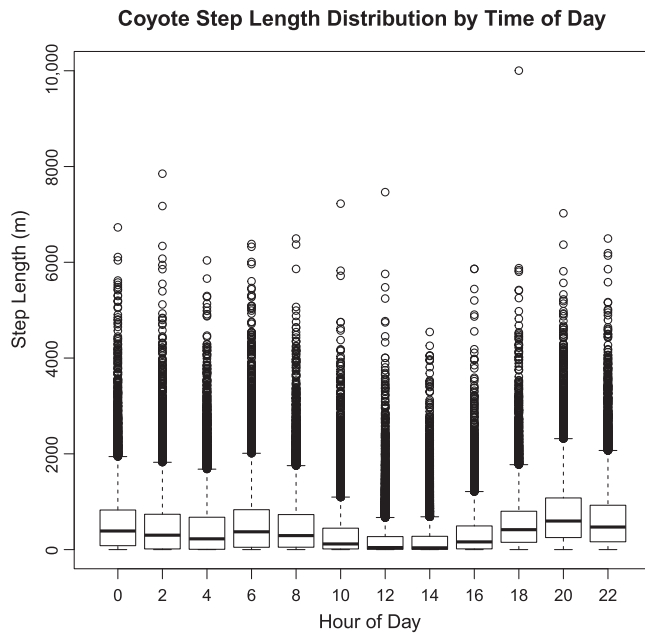
Coyote Step Length Distribution by Time of Day

FIGURE 2　Overall distribution of step lengths by hour of day for coyotes on the San Antonio Viejo Ranch in 2017 and 2018. The *x*-axis represents the hour of day and the *y*-axis represents the length of 2-h steps. Note the pronounced lull in activity in the afternoon, despite high variability
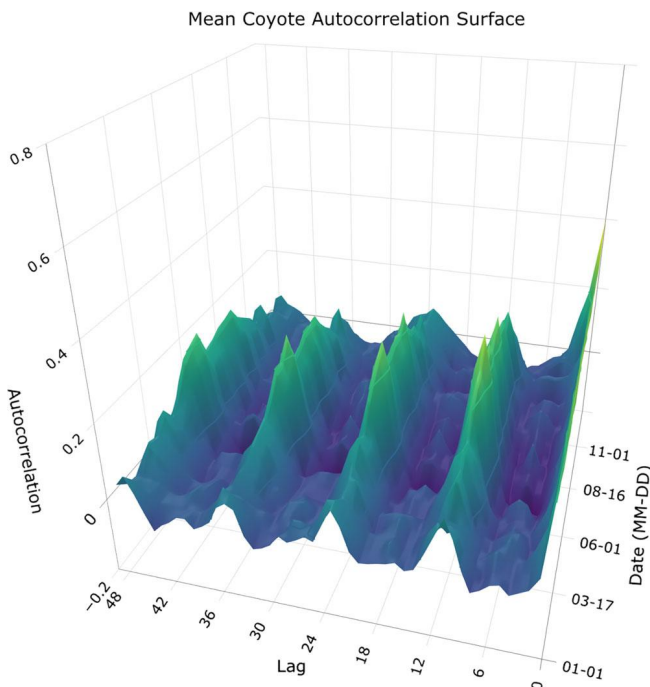
Mean Coyote Autocorrelation Surface

FIGURE 3　The mean coyote autocorrelation surface of coyotes on the San Antonio Viejo Ranch in 2017 and 2018. The *x*-axis represents 2-h time lags, the *y*-axis represents the start date of each 15-day time window, and the *z*-axis represents the autocorrelation in movement velocity. The surface shows a pronounced circadian rhythm in coyote activity, with positive autocorrelation spikes at 12-lag (24-h) intervals. The strength of autocorrelation peaks in mid-May and is weakest in mid-January
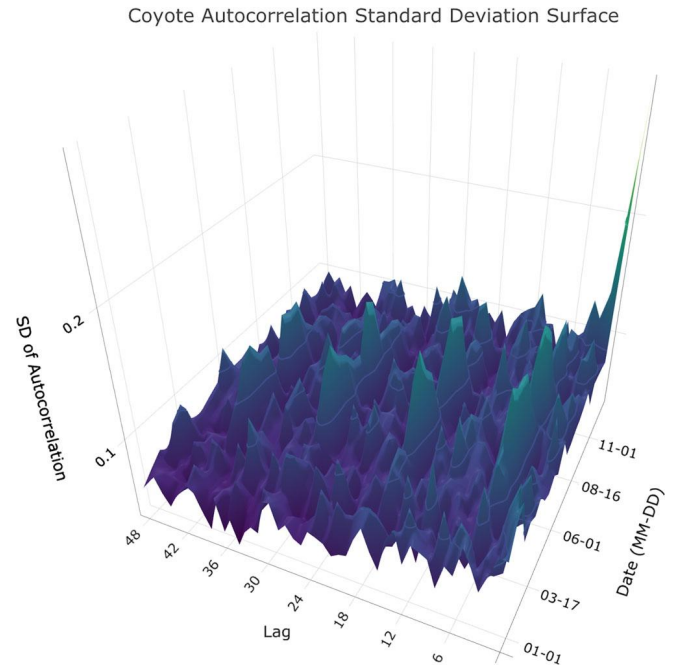
Coyote Autocorrelation Standard Deviation Surface

FIGURE 4　The autocorrelation standard deviation of coyotes on the San Antonio Viejo Ranch, in 2017 and 2018. The *x*-axis represents 2-h time lags, the *y*-axis represents the start date of each 15-day time window, and the *z*-axis represents the standard deviation of autocorrelation in movement velocity. This surface shows two pronounced spikes in variation at crepuscular intervals (6, 18, 30 lags, and so on) in early and late summer, respectively. This is evidence of coyotes diverging between nocturnal and crepuscular activity patterns across individuals

early June (Figure 4). In combination, these surfaces reveal that the dominant, and least variable characteristic in coyote activity is a circadian rhythm while crepuscular behavior is the most variable behavior aspect across individuals, particularly in summer.

Complete linkage clustering revealed at least three distinct groups of activity dynamics (Figure 5). One group consisted of 5 individuals collared in 2016–2017, one contained 6 individuals collared in 2018, and the third contained 21 representing both years. The first group featured a pronounced daily periodicity in activity in summer, but very little evidence of cyclic activity in winter (Figure 6a). The second group showed crepuscular activity, which was weak in the winter, strong in the summer, but faded to a daily cycle in the fall, and was nearly acyclic by the end of the monitoring period (early winter; Figure 6b). The third showed a similar daily cycle to the first group, but was stronger in the winter and weaker in the summer (Figure 6c). The strength of autocorrelation diminished at longer lags more quickly than the first group, indicating that the pattern was less stable within time windows. This behavior represented approximately two thirds of the coyotes monitored across both
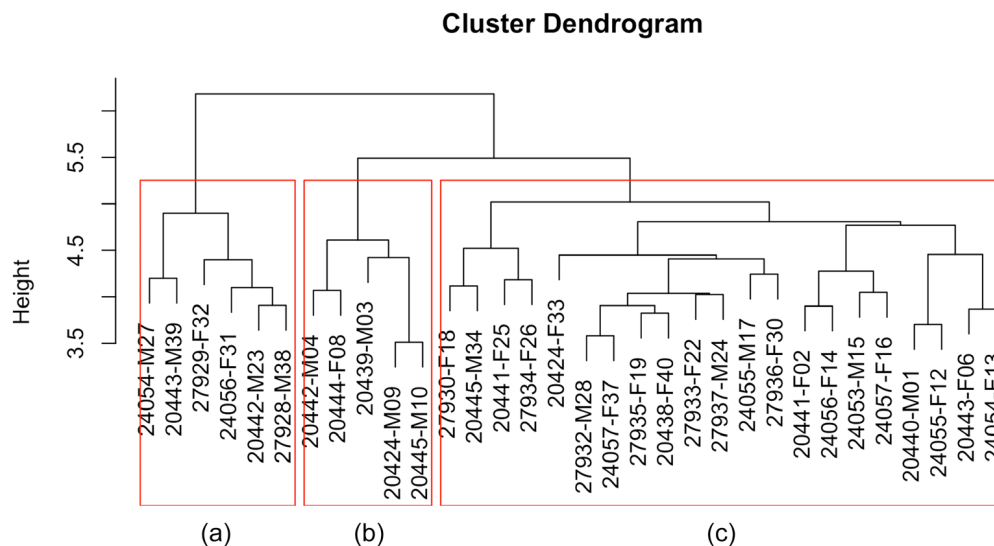
Cluster Dendrogram

F I G U R E 5   Dendrogram of complete linkage clustering of autocorrelation surfaces (ACSs) representing coyotes on the San Antonio Viejo Ranch in 2017 and 2018. Height represents the L^2 Minkowski distance between nodes. Results suggest the existence of at least three groups. The left group (a) contains only coyotes from the second study year while the middle group (b) contains only individuals from the first. The right (c) group contains individuals from both study years. This indicates the existence of at least two patterns of activity dynamics within each year. The mean ACS of each group is presented in Figure 6 with the corresponding group letter

years and was the most common behavior group within each year. PERMANOVA results showed no evidence of sex or size bias in behavior patterns (Table 1). Range size and habitat complexity were not related to similarity in behavior cycles, but study year explained 10.0% of the variance in the distance matrix ($p = 0.001$; Table 1). At a minimum, these results indicate the existence of at least two distinct patterns of activity dynamics in each year within the same population.

DISCUSSION

Our results indicate the dynamics of activity cycles within an unharvested population of coyotes varied by individual. Individuals exhibited divergent nocturnal and crepuscular strategies simultaneously within the study area (Figure 6). Consideration of such variation is lacking in LOF research, despite the recent focus of ethology on interindividual variation and animal personalities (Dingemanse et al., 2009). Overall, autocorrelation was weakest in winter and strongest in the summer (Figure 3; ca. 01-01 and 11-01, and 06-01 on the date axis for winter and summer, respectively). This may be a response to extreme summer heat in this region, which would produce pronounced seasonality in activity patterns. Thus, if we had searched for a dynamic LOF in the winter, we would have been unlikely to find it since predator activity showed little evidence of a predictable temporal cycle. In such a case, the dominant variation in the LOF would be

spatial and consistent with early predictions (Laundre et al., 2001). However, failing to account for temporal variation in risk during the summer would mask real spatial variation in risk that depended on activity cycles (Kohl et al., 2018).

Previous studies suggest that the divergent dynamics we observed may carry different implications for different prey species. Coyote diets in southern Texas are most consistent in winter, focusing on lagomorphs and white-tailed deer (*Odocoileus virginianus*) carrion (Andelt, 1985; Andelt et al., 1987). Activity cycles were consistently weakest in the winter (Figures 3 and 4; ca. 01-01 and 11-01 on the date axis), when food resources are likely most limited. Thus, the magnitude of a LOF may peak in the winter for lagomorphs, but also be relatively constant at daily timescales. This would result in clear spatial patterns of risk because prey would not perceive predator downtimes (sensu Smith et al., 2019) during which they could utilize otherwise risky habitats. Indeed, Arias-Del Razo et al. (2012) observed space use patterns consistent with a LOF with coyotes and lagomorphs in northern Mexico during winter, though their design controlled for cyclicity in risk rather than evaluating it.

Conversely, white-tailed deer fawns are a key component of coyote diets in summer (Andelt, 1985; Andelt et al., 1987), when we observed coyotes diverging between nocturnal and crepuscular behaviors (Figure 4; ca. 06-01 on the date axis). Given strong cyclicity in coyote activity, variation in risk throughout the day would be most predictable by deer during this period. However,
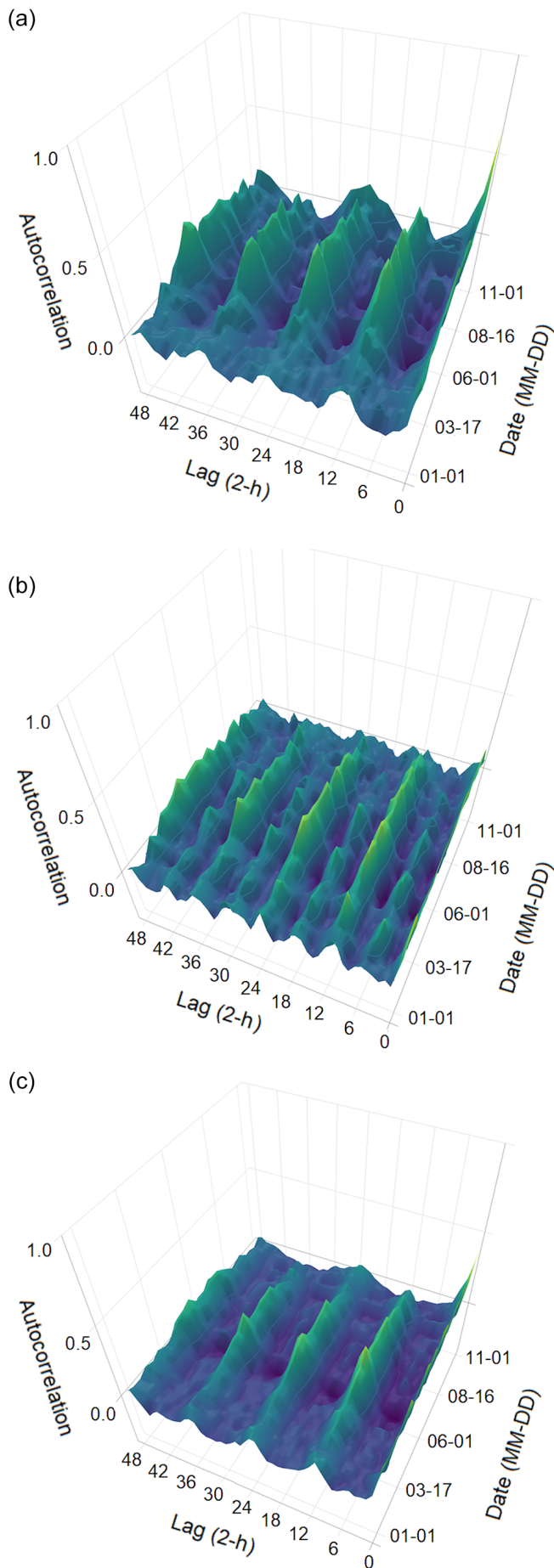
(a)

TABLE 1 Permutational multivariate analysis of variance results examining the influence of range size, sex, body mass, within-range woody canopy cover, and annual conditions on similarity in activity dynamics of coyotes on the San Antonio Viejo Ranch in 2017 and 2018

Estimate	df	SS	R^2	F	Pr(>F)
Range size	1	10.09	0.03	1.04	0.3090
Sex	1	9.52	0.03	0.99	0.4210
Body mass	1	11.05	0.03	1.14	0.1950
Canopy cover	1	11.70	0.04	1.21	0.1320
Year	1	34.48	0.11	3.57	0.0010
Residual	26	251.09	0.77		
Total	31	327.94	1.00		

Note: These results indicate none of the hypothesized predictors of activity dynamics explained appreciable variation in the similarity between autocorrelation surfaces. Year did explain 10.0% of the variation, suggesting at least some coyotes adapted their activity to annual conditions.

(b)

if crepuscular or nocturnal hunting strategies are more effective at catching fawns, the risk posed by a coyote to the fawn will vary by which strategy they use. This is a key question in both predator–prey dynamics, and management literature. The latter provides insight relevant to our example. Does and fawns minimize activity overlap with coyotes at crepuscular hours (Higdon et al., 2019). Further, fawns in southern Texas were shown to avoid activity at crepuscular hours, but not during the day or at night (Jackson et al., 1972). This would minimize activity overlap with crepuscular coyotes, but not with nocturnal ones. If ungulates can distinguish differences in risk

FIGURE 6 Mean autocorrelation surfaces of each of the three behavioral groups identified in our sample of coyotes on the San Antonio Viejo Ranch in 2017 and 2018. These groups were identified by complete linkage clustering, represented in Figure 5. Group letters correspond between both figures. Each surface is rotated to maximize the visibility of important structure. The first group (a) features strong peaks in autocorrelation at daily intervals, indicating a daily activity cycle. The amplitude in autocorrelation peaks in the summer, suggesting that activity cycles are most predictable in that season. There is little evidence of cyclic activity in the winter (front of graph). The second group (b) features strong autocorrelation at half-day intervals, which corresponds to crepuscular activity. The crepuscular rhythms decay to a daily cycle in the late summer and fall. While there is evidence of a weakly crepuscular pattern in winter, autocorrelation peaks in the summer within this group as well. The third group (c) is superficially similar to (a); however, there is evidence of cyclic activity in the winter. Despite this, the overall strength of autocorrelation is weaker within this group for the rest of the year. The amplitude of autocorrelation decreases at longer lags in this group, suggesting that activity cycles were less stable within windows than group (a)

(c)

posed by different coyotes (Gese, 1998), despite their predictability, the overall patterns of summer coyote activity would poorly reflect daily risk dynamics from the perspective of a fawn.

Disentangling which coyotes pose particular risks to certain prey requires reliable predictors of activity cycles. However, we found no evidence of simplistic associations between sex, range size, body size, or woody canopy cover with patterns of activity (Table 1). Thus, commonly hypothesized, simple predictors of activity patterns appear unreliable. Without a way to distinguish drivers of activity patterns, one cannot use convenient activity proxies (e.g., game camera capture rates) to assess perceived risk times if not all predators within a species pose the same risk to a given prey. This makes disentangling activity patterns, and isolating particular predators contributing to a dynamic LOF difficult. Interestingly, we found no relationship between range size, which is linked to territory residency (Kamler & Gipson, 2000), and similarity in activity dynamics. Residency is linked to breeding opportunities and reduced mortality risk (Gese et al., 1988; Windberg, 1995), indicating no strong linkages between this host of variables and activity dynamics. This suggests that any influences of territoriality on activity may depend on the dynamic nature of space use (Morin & Kelly, 2017), as well as that of activity cycles.

Other factors that we did not capture, however, may drive activity dynamics. Group membership may explain similarity in activity dynamics; however, capturing this influence may be complex. While two pairs of collared coyotes did occur within social groups for an extended period of the study, group membership was otherwise dynamic and other co-occupancy between collared individuals was fleeting. Because of this, linking dynamic group membership to dynamic activity patterns is not straightforward and likely requires more data than were available at the time of this study. Social rank within a territorial group is believed to affect behavioral responses of individuals to resource limitation (Polansky et al., 2013), which is known to influence several aspects of coyote behavior (Bekoff & Wells, 1982). However, social rank is difficult to study in semi-cryptic carnivores, particularly habitats with dense vegetation, due to limited visibility and confounding effects of observer presence (Bekoff & Wells, 1986). Thus, we were unable to evaluate the effect of coyote social rank within a social group on behavior. Interestingly, the first group revealed in our clustering showed a considerably more abrupt change from acyclic winter behavior to a strong daily cycle in spring, which may correspond to breeding (Bekoff & Gese, 2003). It is possible that these individuals shifted behavior to whelp or assist with rearing pups (Bekoff &

Wells, 1986), thus this pattern could potentially be linked to alpha or beta status within a social group.

Further, while we were able to show that individuals within a population diverged in activity patterns, we could not directly assess whether this was related to their choice of prey or their mode of hunting in this study. Both of these constraints may be alleviated by rapidly developing video bio-logging technology (de la Rosa, 2019). Video data would provide needed information on social interactions as well as prey choice without biases associated with human observers. This information could be used in conjunction with our methodology to evaluate relationships between activity dynamics, social rank, and foraging strategy. Video data may also allow testing whether movement activity is a reliable predictor of a predator's risk to a prey species. While most studies assume that movement activity does serve well as a risk predictor (Kohl et al., 2018), this may not be the case in some circumstances. For example, in vision-based hunters, success may depend on external conditions, such as light levels or visibility in a given habitat. In such a case, lethality may be decoupled from activity. Video data would allow direct comparisons between movement activity and dynamics of predator lethality as predictors of LOF dynamics.

In either case, using species-level activity patterns as a proxy for temporal variation in predation risk assumes that the mean activity pattern is representative of individuals that prey on the prey species of interest. However, the mean activity pattern may poorly predict dynamics if behavior patterns diverge across individuals. This has long been recognized in carnivore behavior research (Gittleman & Harvey, 1982), and is relevant to LOFs when the groups of activity patterns represent predators with different foraging strategies. Our results suggest that trends and intraspecific variation in predator activity cycles should be taken into account in LOF research.

The LOF concept is a unifying idea, bridging animal behavior, habitat selection, movement, and population dynamics. It has great potential as both a theoretical and heuristic tool, as well as implications for generating spatio-temporally targeted management solutions to predator issues. However, to realize the potential of the LOF, we must not overlook critical aspects of predator ecology with simple assumptions. Acknowledging the role of differential behavior within predator populations further advances the concepts utility. We demonstrated the complexity and interindividual variation in coyote behavior, and argue that its explicit consideration will further aid the LOF concept in explaining the complexity of predator–prey dynamics. Acknowledging and accounting for intraspecific differences in activity will reduce unmodeled error in studies of LOF dynamics, perhaps clarifying equivocal support in previous work. By considering intraspecific behavioral variation

explicitly, we can gain a much clearer picture of the complexity, drivers, and ecological effects of fear.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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REFERENCES

Alanara, A., M.D. Burns, and N.B. Metcalfe. 2001. "Intraspecific Resource Partitioning in Brown Trout: The Temporal Distribution of Foraging is Determined by Social Rank." *Journal of Animal Ecology* 70: 980–6.

Andelt, W.F. 1985. "Behavioral Ecology of Coyotes in South Texas." *Wildlife Monographs* 94: 1–45.

Andelt, W.F., J.G. Kie, F.F. Knowlton, and K. Cardwell. 1987. "Variation in Coyote Diets Associated with Season and Successional Changes in Vegetation." *Journal of Wildlife Management* 51: 273–7.

Anderson, M.J. 2001. "A New Method for Non-Parametric Multivariate Analysis of Variance." *Austral Ecology* 26: 32–46.

Arias-Del Razo, I., L. Hernandez, J.W. Laundre, and O. Meyers. 2011. "Do Predator and Prey Foraging Activity Patterns Match? A Study of Coyotes (*Canis latrans*), and Lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*)." *Journal of Arid Environments* 75: 112–8.

Arias-Del Razo, I., L. Hernandez, J.W. Laundre, and L. Velasco-Vazquez. 2012. "The Landscape of Fear: Habitat Use by a Predator (*Canis latrans*) and its Main Prey (*Lepus californicus* and *Sylvilagus audobonii*)." *Canadian Journal of Zoology* 90: 683–93.

Bekoff, M., and E.M. Gese. 2003. "Coyote: *Canis latrans*." In *Wild Mammals of North America: Biology, Management, and Conservation*, 2nd ed., edited by O.A. Feldhamer, B.C. Thompson, and J.A. Chapman, 467–81. Baltimore, MD: Johns Hopkins University Press.

Bekoff, M., and M.C. Wells. 1982. "Behavioral Ecology of Coyotes: Social Organization, Rearing Patterns, Space Use, and Resource Defense." *Zeitschrift für Tierpsychologie* 60: 281–305.

Bekoff, M., and M.C. Wells. 1986. "Social Ecology and Behavior of Coyotes." *Advances in the Study of Behavior* 16: 251–338.

Berger-Tal, O., T. Polak, A. Oron, Y. Lubin, B.P. Kotler, and D. Saltz. 2011. "Integrating Animal Behavior and Conservation Biology: A Conceptual Framework." *Behavioral Ecology* 22: 236–9.

Bliecher, S.S. 2017. "The Landscape of Fear Conceptual Framework: Definition and Review of Current Applications and Misuses." *PeerJ* 5: 1–22.

Boisjoly, D., J. Oullet, and R. Courtios. 2010. "Coyote Habitat Selection and Implications for the Gaspesie Caribou." *Journal of Wildlife Management* 74: 3–11.

Boyce, M.S., J. Pitt, J.M. Northrup, A.T. Morehouse, K.H. Knopff, B. Cristescu, and G.B. Stenhouse. 2010. "Temporal Autocorrelation Functions for Movement Rates from Global Positioning System Radiotelemetry Data." *Philisophical Transactions of the Royal Society B: Biological Sciences* 365: 2213–9.

Calenge, C., S. Dray, and M. Royer-Carenzi. 2009. "The Concept of Animals' Trajectories from a Data Analysis Perspective." *Ecological Informatics* 4: 34–41.

Campbell, J.B., and R.H. Wynne. 2011. *Introduction to Remote Sensing*, 5th ed. New York: Guilford Press.

Cushman, S.A., M. Chase, and C. Griffin. 2005. "Elephants in Space and Time." *Oikos* 109: 331–41.

Dingemanse, N.J., A.J.N. Kazem, D. Reale, and J. Wright. 2009. "Behavioural Reaction Norms: Animal Personality Meets Individual Plasticity." *Trends in Ecology & Evolution* 25: 81–9.

Dodson, S. 1990. "Predicting Diel Vertical Migration of Zooplankton." *Limnology and Oceanography* 35: 1195–200.

Eriksen, A., P. Wabakken, B. Zimmermann, H.P. Andreassen, J.M. Arnemo, H. Gundersen, O. Liberg, et al. 2011. "Activity Patterns of Predator and Prey: A Simultaneous Study of GPS-Collared Wolves and Moose." *Animal Behaviour* 81: 423–31.

Gese, E.M. 1998. "Threat of Predation: Do Ungulates Behave Aggressively towards Different Members of a Coyote Pack?" *Canadian Journal of Zoology* 77: 499–503.

Gese, E.M., O.J. Rongstad, and W.R. Mytton. 1987. "Manual and Net-Gun Capture of Coyotes from Helicopters." *Wildlife Society Bulletin* 15: 444–5.

Gese, E.M., O.J. Rongstad, and W.R. Mytton. 1988. "Population Dynamics of Coyotes in Southeastern Colorado." *Journal of Wildlife Management* 53: 174–81.

Gipson, P.S., and J.A. Sealander. 1972. "Home Range and Activity of the Coyote (*Canis latrans frustror*) in Arkansas." *Proceedings of the Annual Conference of Southeastern Association of Game and Fish Commissioners* 26: 82–95.

Gittleman, J.L., and P.H. Harvey. 1982. "Carnivore Home-Range Size, Metabolic Needs and Ecology." *Behavioral Ecology and Sociobiology* 10: 57–63.

Higdon, S.D., C.A. Diggins, M.J. Cherry, and W.M. Ford. 2019. "Activity Patterns and Temporal Predator Avoidance of White-Tailed Deer (*Odocoileus virginianus*) during Fawning Season." *Journal of Ethology* 37: 283–90.

Hinton, J.W., J.L. Gittleman, F.T. van Manen, and M.J. Chamberlain. 2018. "Size-Assortative Choice and Mate Availability Influences Hybridization between Red Wolves (*Casis rufus*) and Coyotes (*Canis latrans*)." *Ecology and Evolution* 8: 3927–40.

Holzman, S., M.J. Conroy, and J. Pickering. 1992. "Home Range, Movements, and Habitat Use of Coyotes in Southcentral Georgia." *Journal of Wildlife Management* 56: 139–46.

Jackson, R.M., M. White, and F.F. Knowlton. 1972. "Activity Patterns of Young White-Tailed Deer Fawns in South Texas." *Ecology* 53: 262–70.

Kamler, J., and P.S. Gipson. 2000. "Space and Habitat Use by Resident and Transient Coyotes." *Canadian Journal of Zoology* 78: 2106–11.

Kitchen, A.M., E.M. Gese, and E.R. Schauster. 2000. "Changes in Coyote Activity Patterns Due to Reduced Exposure to Human Persecution." *Canadian Journal of Zoology* 78: 853–7.

Knowlton, F.F. 1972. "Preliminary Interpretations of Coyote Population Mechanics with Some Management Implications." *Journal of Wildlife Management* 36: 369–82.

Kohl, M.T., D.R. Stahler, M.C. Metz, J.D. Forester, M.J. Kauffman, N. Varley, P.J. White, D.W. Smith, and D.R. MacNulty. 2018. "Diel Predator Activity Drives a Dynamic Landscape of Fear." *Ecological Monographs* 88: 638–52.

Lance, G.N., and W.T. Williams. 1967. "A General Theory of Classificatory Sorting Strategies 1. Hierarchical Systems." *The Computer Journal* 9: 373–80.

Lank, D.B., and R.C. Ydenberg. 2003. "Death and Danger at Migratory Stopovers: Problems with with 'Predation Risk'." *Journal of Avian Biology* 34: 225–8.

Laundre, J.W., L. Hernandez, and K.B. Altendorf. 2001. "Wolves, Elk, and Bison: Reestablishing the 'Landscape of Fear' in Yellowstone National Park, U.S.A." *Canadian Journal of Zoology* 79: 1401–9.

Legendre, P., and L. Legendre. 1998. *Numerical Ecology*, 2nd ed. Amsterdam: Elsevier Science.

Lucherini, M., J.I. Reppucci, R.S. Walker, M.L. Villalba, A. Wurstten, G. Gallardo, A. Iriarte, R. Villalobos, and P. Perovic. 2009. "Activity Pattern Segregation of Carnivores in the High Andes." *Journal of Mammalogy* 90: 1404–9.

Montero, P., and J.A. Vilar. 2014. "TSclust: An R Package for Time Series Clustering." *Journal of Statistical Software* 62: 1–43.

Morin, D.J., and M.J. Kelly. 2017. "The Dynamic Nature of Territoriality, Transience, and Biding in an Exploited Coyote Population." *Wildlife Biology* 2017: 1–13.

Moritz, S., and T. Bartz-Beielstein. 2017. "imputeTS: Time Series Missing Value Imputation in R." *The R Journal* 9: 207–18.

Morosinotto, C., R.L. Thomson, and E. Korpimaki. 2010. "Habitat Selection as an Antipredator Behaviour in a Multi-Predator Landscape: All Enemies Are Not Equal." *Journal of Applied Ecology* 79: 327–33.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., et al. (2019). *vegan: Community Ecology Package. R package version 2.5-4*. https://CRAN.R-project.org/package=vegan

Palmer, M.S., J. Fieberg, A. Swanson, M. Kosmala, and C. Packer. 2017. "A 'Dynamic' Landscape of Fear: Prey Responses to Spatiotemporal Variations in Predation Risk across the Lunar Cycle." *Ecology Letters* 20: 1364–73.

Polansky, L., I. Douglas-Hamilton, and G. Whittemyer. 2013. "Using Diel Movement Behavior to Infer Foraging Strategies Related to Ecological and Social Factors in Elephants." *Movement Ecology* 1: 1–13.

Preisser, E.L., D.I. Bolnick, and M.F. Benard. 2005. "Scared to Death? The Effects of Intimidation and Consumption in Predator–Prey Interactions." *Ecology* 86: 501–9.

R Core Team. 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramsay, J.O., and B.W. Silverman. 2002. *Applied Functional Data Analysis*. New York: Springer Series in Statistics. Springer.

de la Rosa, C.A. 2019. "An Inexpensive and Open-Source Method to Study Large Terrestrial Animal Diet and Behaviour Using Time-Lapse Video and GPS." *Methods in Ecology and Evolution* 10: 615–25.

Sacks, B.N., M.M. Jaeger, J.C.C. Neale, and D.R. McCullough. 1999. "Territoriality and Breeding Status of Coyotes Relative to Sheep Predation." *Journal of Wildlife Management* 63: 593–605.

Sacks, B.N., and J.C.C. Neale. 2007. "Coyote Abundance, Sheep Predation, and Wild Prey Correlates Illuminate Mediterranean Trophic Dynamics." *Journal of Wildlife Management* 71: 2404–11.

Schmidt, K., and D.P.J. Kuijper. 2015. "A 'Death Trap' in the Landscape of Fear." *Mammal Research* 60: 275–84.

Slayter, R.A., M. Hirst, and J.P. Sexton. 2013. "Niche Breadth Predicts Geographical Range Size: A General Ecological Pattern." *Ecology Letters* 16: 1104–14.

Smith, J.A., E. Donadio, J.N. Pauli, M.J. Sheriff, and A.D. Middleton. 2019. "Integrating Temporal Refugia into Landscapes of Fear: Prey Exploit Predator Downtimes to Forage in Risky Places." *Oecologia* 189: 883–90.

Thibault, I., and J.P. Ouellet. 2005. "Hunting Behaviour of Eastern Coyotes in Relation to Vegetation Cover, Snow Conditions, and Hare Distribution." *Ecoscience* 12: 466–75.

Thompson, C.M., J.A. Royle, and J.D. Garner. 2012. "A Framework for Inference about Carnivore Density from Unstructured Spatial Sampling of Scat Using Detector Dogs." *Journal of Wildlife Management* 76: 863–71.

Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, MA: Sinauer Associates.

Venables, W.N., and B.D. Ripley. 2002. *Modern Applied Statistics with S*, 4th ed. New York: Springer.

Ward, J.N., J.W. Hinton, K.L. Johannsen, M.L. Karlin, K.V. Miller, and M.J. Chamberlain. 2019. "Home Range Size, Vegetation Density, and Season Influences Prey Use by Coyotes (*Canis latrans*)." *PLoS One* 13: 1–22.

Way, J.G., I.M. Ortega, and E.G. Stauss. 2004. "Movement and Activity Patterns of Eastern Coyotes in a Coastal, Suburban Environment." *Northeastern Naturalist* 11: 237–54.

Way, J.G., and B.N. White. 2013. "Coyotes, Red Foxes, and the Prevalence of Lyme Disease." *Northeastern Naturalist* 20: 655–65.

Windberg, L.A. 1995. "Demography of a High-Density Coyote Population." *Canadian Journal of Zoology* 73: 942–54.

Woodruff, R.A., and B.L. Keller. 1982. "Dispersal, Daily Activity, and Home Range of Coyotes in Southeastern Idaho." *Northwest Science* 56: 199–207.

Worton, B.J. 1989. "Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies." *Ecology* 70: 164–8.

Yang, H., S. Han, B. Xie, P. Mou, X. Kou, T. Wang, J. Ge, and L. Feng. 2018. "Do Prey Availability, Human Disturbance, and Habitat Structure Drive the Daily Activity Patterns of Amur Tigers (*Panthera tigris altaica*)?" *Journal of Zoology* 307: 131–40.

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