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Abiotic variables influencing the nocturnal movements of bobcats and coyotes

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Despite the increasing spatial, temporal and dietary overlap between bobcats *Lynx rufus* and coyotes *Canis latrans*, these species live sympatrically throughout much of North America. To determine if differential activity patterns relative to abiotic variables might influence interspecific interactions, we investigated whether these species responded differentially to crepuscular and nocturnal abiotic variables in Texas. Using GPS collars, we calculated hourly movements from sequential locations, and compared bobcat and coyote movements relative to sex, season, moonlight intensity, night period, crepuscularity and temperature. We used generalized linear mixed effects models (GLMM) to investigate the responses of bobcats and coyotes to variables associated to their nocturnal movements. Temperature and its interactions with various abiotic variables influenced bobcat movements. Biological season and its interactions with other abiotic variables influenced coyote movements. Bobcats moved shorter hourly distances than coyotes. Female bobcats moved shorter hourly distances than males. Moonlight intensity seemed to influence coyotes but not bobcats. Differential movements between bobcats and coyotes relative to night period could possibly be due behavioral avoidance of coyotes by bobcats. Reduced crepuscular activity by coyotes may be behavioral avoidance of humans. Differential responses to nocturnal variables may dampen competitive interactions between bobcats and coyotes.

Keywords: activity, biological season, bobcat, *Canis latrans*, coyote, crepuscular, GLMM, *Lynx rufus*, moonlight intensity, movement, nocturnal, temperature

Where species with similar resource requirements live sympatrically it is likely that those species adopt differential activity patterns to dampen possible competitive interactions (Schoener 1974, Litvaitis and Harrison 1989). Terrestrial mammals may be categorized into one of four temporal activity classes: diurnal, nocturnal, crepuscular and cathemeral (Bennie et al. 2014, Ikeda et al. 2016). In addition to various physical constraints, factors such as day and night length, temperature, rainfall, competition and anthropogenic behavior influence activity patterns (Ikeda et al. 2016).

Activity patterns are governed primarily by nutrition and reproduction. Sympatric, highly interactive species manage their activity to maximize their nutritional and reproductive mandates, and to limit aggressive intraguild interactions (Arias-Del Razo et al. 2011).

Activity patterns are not only influenced by competitive interactions, but also by species' endogenous clocks (Kronfeld-Schor and Dayan 2003) and prey activity (Arias-Del Razo et al. 2011, Monterroso et al. 2014). Predator circadian activity is often shaped by the temporal availability of prey (Halle 2000, Monterroso et al. 2013, Broekhuis et al. 2014). Specialist predators synchronize their activity with preferred prey, while generalist predators' activity is less closely linked to specific prey (Monterroso et al. 2013). Moonlight and lunar cycle influence animal behavior (Clarke 1983, Pratas-Santiago et al. 2016). Visual predators are thought to be more active around full moon because increased illumination correlates with increased prey detection and foraging efficiency (Prugh and Golden 2014). However, increased illumination also improves the ability of prey to detect and avoid predators (Penteriani et al. 2013, Prugh and Golden 2014).

Temperature influences animal behavior (Murray and Smith 2012). Most species vary their activity relative to temperature, and typically operate well within their physiological thermal tolerance range (Magnuson et al. 1979). Lethal limits set ultimate constraints on thermal tolerance (Bennie et al. 2014). Bobcats *Lynx rufus* (Bailey 1974) and coyotes *Canis latrans* (Shivik et al. 1997) tend to travel shorter distances during cooler seasons.

Bobcats and coyotes are sympatric over much of North America (Nowak 1999, Neale and Sacks 2001, Kays and Wilson 2009, Witczuk et al. 2015). Despite coyotes being hierarchically superior predators (Bunnell et al. 2007, Witczuk et al. 2015), coyotes and bobcats compete for many resources (Neale and Sacks 2001, Thornton et al. 2004). Interactions between bobcats and coyotes manifest at both the population and individual level and are context-dependent. For example, bobcat populations tend to be declining when associated with range expansion of coyotes (Litvaitis and Harrison 1989, Witczuk et al. 2015), and both species experience inverse trajectories of population indices (Linhart and Robinson 1972, Neale and Sacks 2001). Bobcat populations increased after coyote removal (Henke and Bryant 1999, Neale and Sacks 2001), which may have been due to reduced intraguild predation by coyotes (Knick 1990, Neale and Sacks 2001, Melville et al. 2015a). In other instances, the interactions between coyote and bobcat abundance patterns are neutral (Lovell et al. 1998, Main et al. 1999) or positive (Schnell et al. 1985, Neale and Sacks 2001).

Bobcats and coyotes use similar prey (Litvaitis and Harrison 1989, Fedriani et al. 2000, Thornton et al. 2004, Melville et al. 2015a, Witczuk et al. 2015) – predominantly hispid cotton rats *Sigmodon hispidus*, eastern cottontail rabbits *Sylvilagus floridanus* and white-tailed deer *Odocoileus virginianus* in east Texas (Melville et al. 2015a). Their dietary overlap is greatest when food is most limiting (Fedriani et al. 2000). Periodically, interspecific competition for food is amplified to the detriment of bobcats, due to their more restricted and temporally variable diets (Fedriani et al. 2000, Gompper 2002, Melville et al. 2015a).

Spatial overlap of coyotes and bobcats is increasing (Gompper 2002, Thornton et al. 2004, Levy 2012). Historically, coyotes' range was restricted to the southwestern and plains regions of the United States and Canada, and northern and central Mexico. Coyote range is expanding south and east in synchrony with land use change and the extirpation of gray wolves *Canis lupus*, especially since 1900 (MacDonald and Sillero-Zubiri 2007). Locally, bobcat and coyote home ranges overlap (Witmer and de Calesta 1986, Major and Sherburne 1987, Litvaitis and Harrison 1989, Chamberlain 1999, Thornton et al. 2004, Melville et al. 2015b). Spatial overlap between bobcats and coyotes may be mitigated by differential habitat selection (Thornton et al. 2004, Witczuk et al. 2015), however, this only manifests at finer scales (Chamberlain et al. 2000, 2003, Chamberlain and Leopold 2005), and may be more temporally linked than previously thought. Although coyotes may display levels of cathemeral activity (Chamberlain et al. 1998), bobcats and coyotes are primarily nocturnal or crepuscular (Witmer and de Calesta 1986, Thornton et al. 2004), especially in fragmented habitat (Tigas et al. 2002). The substantial temporal overlap in activity patterns between these species might amplify the potential for interspecific competition.

As bobcats and coyotes use similar prey, inhabit similar areas and are predominantly crepuscular and nocturnal, an analysis of abiotic variables associated with their nocturnal activity patterns might shed light on mechanisms that allow these species to avoid competition. The aim of this study was to investigate how nocturnal movement distances of male and female bobcats and coyotes varied as function of seasons, moonlight intensity, night portion and temperature. As our study represents a sympatric situation, it may not only provide information about the two species' activity patterns in relation the temporal predictors, but also hint at possible strategies to minimize inter-specific activity overlap.

Study area

We conducted this study from January 2009 to July 2011 on a 1360 ha private pine plantation (31°31′57.2″N, 94°42′91.2″W), and a 5000 ha commercial timber property (31°21′28.1″N, 94°24′54.4″W) in Nacogdoches and Angelina counties in east Texas. The vegetation resembles the southeastern mixed and southeastern coniferous forests. Longleaf pine *Pinus palustris* forests have largely been replaced by even-aged loblolly pine *P. taeda* plantations. The natural vegetation has been transformed by the planting of pine stands and the exclusion of fire (Omernick et al. 2008). The topography is undulating hills with swampy low-lying areas. Historically these pine forests were successional to hardwood forests. The mean annual rainfall in the Pineywoods is 1192 mm, with monthly means from 55 mm in July to 116 mm in May (NOAA 2012). The temperatures vary from > 38°C in summer to < −5°C in winter.

Methods

We trapped from 1 January to 30 April in each year of the study. We used padded leg-hold traps (Victor soft-catch no. 3) to capture 10 bobcats (four males in 2009, one female and one male in 2010 and two females and two males in 2011) (Melville et al. 2015b) and 10 coyotes (one female and two males in 2009, two females and two males in 2010 and one female and two males in 2011) (Grinder and Krausman 2001, Melville et al. 2015b). We immobilized captured animals with appropriate doses ($6\,\mathrm{mg\,kg^{-1}}$ for bobcats and $5\,\mathrm{mg\,kg^{-1}}$ for coyotes) of TELAZOL (<www.fortdodge.eu>). While they were sedated, we fitted each animal with a Televilt Tellus GPS collar (<tellus.televilt.se>). We programmed each collar to record hourly locations from 17:00 to 07:00. All animal capture and processing protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011).

We used two definitions of season: the Natural (Astronomical) Seasons (winter: 21 December to 20 March, spring: 21 March to 20 June, summer: 21 June to 20 September, fall: 21 September to 20 December) (Chamberlain et al. 1998, Kirby et al. 2010, Melville et al. 2015b), and the Biological seasons: spring (1 February to 31 May, bobcat and coyote breeding season), summer (1 June to 30 September, bobcat kitten rearing season, coyote post nursing period) and winter (1 October to 31 January, coyote pre-breeding) (Andelt and Gipson 1979, Andelt 1985, Chamberlain et al. 2000, 2003).

For analysis of bobcat and coyote response to lunar light we allocated a Moonlight intensity value to each hourly movement (US Naval Observatory, URL: <www.public.navy.mil/fltfor/cnmoc/Pages/usno_test_page.aspx>). We modelled the Moonlight intensity (the percentage of the moon face visible) as a continuous variable from 0% to 100%. Cloud cover impacts nocturnal illumination (Hahn et al. 1995, Kyba et al. 2011, Rockhill et al. 2013), however, we assumed that cloud cover effect would be consistent throughout the year and excluded it as a variable.

We divided night time into three periods, evening (17:00–22:00 h), night (22:01–02:00 h) and morning (02:01–07:00 h). We defined Crepuscularity as the period one hour before and after both sunset and sunrise (Rockhill et al. 2013, Pratas-Santiago et al. 2016). Collar data were time-stamped relative to Greenwich mean time (GMT) and we made no adjustments for daylight saving (times are all GMT – 5 h). The collars had thermometers integrated into the housings and, although these did not strictly measure ambient temperature, they gave a reasonable indication of the temperature perceived by the animal (Samuelsson, Televilt/Followit, pers. comm.). We modelled collar measured temperatures as a continuous variable.

Data analysis

We calculated the linear distance between consecutive nocturnal locations, for each animal, using the Pythagorean formula:

$$\text{Distance}(m) = \sqrt{\left(\text{UTM northing}\,1 - \text{UTM northing}\,2\right)^2 + \left(\text{UTM easting}\,1 - \text{UTM easting}\,2\right)^2}$$

We used linear displacement as a proxy for distance moved each hour (hereafter 'movement'; Palomares and Delibes 1991, Rockhill et al. 2013). Each movement was associated with Sex, Astronomical season, Biological season, Lunar phase, Moonlight intensity, Night period, Crepuscularity and Temperature. Prior to analysis, we removed movement intervals that had missing variables from the data sets.

From collar data, we calculated 11 940 ($\bar{x} = 1194$) discrete movement intervals for bobcats (3530 for females ($\bar{x} = 1177$) and 8410 for males ($\bar{x} = 1201$)) and 12 701 ($\bar{x} = 1270$) for coyotes (5695 for females ($\bar{x} = 1424$), and 7006 for males ($\bar{x} = 1167$)). Coyotes moved farther each hour than bobcats. Bobcat movements varied from 0.6 to 2059 m h^{-1} ($\bar{x} = 230$ m h^{-1}, n = 11 935, SE = 2.39), while coyote movements varied from 0.2 to 4636 m h^{-1} ($\bar{x} = 336$ m h^{-1}, n = 12 686, SE = 4.18).

We used generalized linear mixed effects models (GLMMs) (Bolker et al. 2009, Harrison et al. 2018) to model hourly movements relative to nocturnal variables. We used the distance moved (m h^{-1}) as the dependent variable, the variables Astronomical season, Biological season, Moonphase, Moonlight intensity, Night period, Crepuscular period and Temperature as fixed effects and the individual animals as random effects (Harrison et al. 2018). This obviated any concerns of autocorrelation between consecutive data points (Harrison et al. 2018). We used program R (<www.r-project.org>) and the packages 'lme4' (Bates et al. 2015), 'lmerTest' (Kuznetsova et al. 2017) and 'emmeans' (Lenth 2019) to model the effects of variables associated with bobcat and coyote movements. Visual assessment of the data suggested that the residuals were not normally distributed, consequently we identified the most appropriate data transformation using the 'bestNormalize' package (Peterson and Cavanaugh 2019) in program R. This identified the ordered quantile normalization transformation (Peterson and Cavanaugh 2019) as most appropriate for all three data sets. We applied this transformation to 'distance moved', for each of our data sets (bobcat movements, coyote movements and the combined bobcat and coyote movements). After transformation the residuals were normally distributed, and we performed our analyses on the transformed data.

We suspected that some variables might be collinear, particularly Astronomical season with Biological season and Moon phase with Moonlight intensity. To avoid inferential errors associated with collinearity, we the calculated variable inflation factors (VIF) for each independent variable. Where variables had VIF ≥ 3 (Zuur et al. 2010, Thompson et al. 2017), we dropped one of the collinear variables from our candidate set. We used the bobcat data to refine the variable set and then checked the VIF values for the coyote and the combined data sets.

Having defined our candidate variables, we used model selection to identify the combination of variables best supported by our data using the corrected Akaike's information criterion (AICc) (Hurvich and Tsai 1989). We calculated the AICc values of each independent variable and used these to establish a hierarchy of influence within each candidate set of variables. We started with the full model (all variables included) and then sequentially removed the variable with the highest AICc score from the model. The sequence in which we removed variables from bobcat models was: 1) Moonlight intensity, 2) Sex, 3) Crepuscularity, 4) Biological season, 5) Night period and 6) Temperature. The sequence of variable removal from coyote models was: 1) Sex, 2) Night period, 3) Moonlight intensity, 4) Biological season, 5) Crepuscularity and 6) Temperature. The sequence of variable removal from the combined model was: 1) Species, 2) Sex, 3) Moonlight intensity, 4) Biological season, 5) Night period, 6) Crepuscularity and 7) Temperature. In addition, we evaluated each combination of two-way variable interactions. Where models contained interactions, we started with a model containing all two-way interactions and then applied the same hierarchical removal of variables from the models. For models that contained both species, only interactions of the variable 'Species' with other variables was considered. In all cases, delta AICc scores greater than six were considered to have substantially less support than the best model (Harrison et al. 2018). We calculated marginal and conditional R^2 values for each model (Nakagawa and Schielzeth 2013). The marginal R^2 values represent the variance attributable to the fixed effects and the conditional R^2 values relate to the variance explained by the entire models (Nakagawa and Schielzeth 2013).

Results

There was evidence in the bobcat data of collinearity between Moon phase and Moonlight intensity (Moon phase VIF = 6.75, Moonlight intensity VIF = 6.74), and between Astronomical and Biological seasons (Astronomical season VIF = 6.24, Biological season VIF = 6.29). By dropping Moon phase and Astronomical season from the candidate set, all VIF values fell below 3 (Zuur et al. 2010, Thompson et al. 2017).

Bobcats

Female bobcats consistently moved shorter distances ($\bar{x} = 160\,\mathrm{m\,h^{-1}}$, n = 3, SE = 62) than males ($\bar{x} = 236\,\mathrm{m\,h^{-1}}$, n = 7, SE = 43). Bobcat movements tended to increase from the breeding season through the kitten rearing season ($t = -4.40$, df = 11 910, $p < 0.001$) and winter ($t = -4.06$, df = 1910, $p < 0.001$) (Fig. 1) (Supplementary material Appendix 1 Table A1). This trend was consistent between sexes, variation in seasonal movement was significant for females between the breeding and kitten rearing seasons ($t = -6.03$, df = 3528.94, $p < 0.001$), however male movement differed between breeding season and the kitten rearing season ($t = -1.96$, df = 8383.18, $p = 0.05$) and between the breeding season and winter ($t = -3.95$, df = 8383.03, $p < 0.001$) (Supplementary material Appendix 1 Table A1). Bobcat movements were not greatly influenced by Moonlight intensity ($t = -0.52$, df = 11 900, $p = 0.61$) (Fig. 2) (Supplementary material Appendix 1 Table A1). Night period influenced bobcat movements (Fig. 3) decreasing from the period prior to 22:00 through to 02:00 h ($t = -10.89$, df = 11 900, $p < 0.001$), but then increasing between 02:01 and 07:00 h ($t = -7.48$, df = 11 900, $p < 0.001$). Generally, bobcats moved marginally farther in the crepuscular period than during the night (Fig. 4) (Supplementary material Appendix 1 Table A1). This pattern was not consistent for males and females. Females moved farther in the night than in the crepuscular period (although not significantly so) whereas males moved farther in the crepuscular period ($t = 3.25$, df = 8378, $p = 0.001$) (Supplementary material Appendix 1 Table A1). Bobcats movements declined as temperature increased ($t = -26.84$, df = 11 910, $p < 0.001$) (Fig. 5).

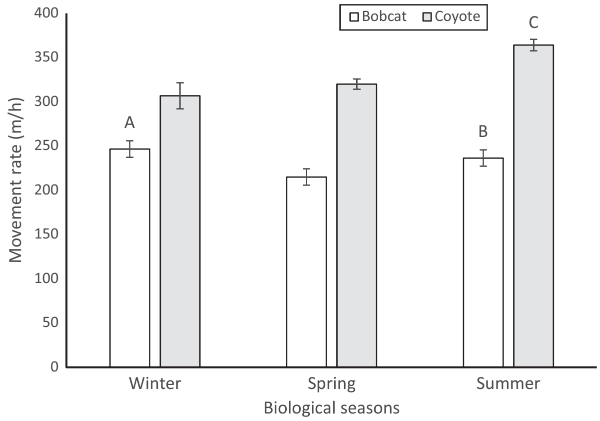

Figure 1. Rates of movement (± 1 SE) by bobcats *Lynx rufus* and coyotes *Canis latrans* relative to biological seasons in east Texas from January 2009 to July 2011. A, B, C = Statistically significant influence of biological seasons within species (Supplementary material Appendix 2 Output A1).

Temperature and its interaction with Sex, Biological season, Night portion and Crepuscularity was the model best supported by our data (Model 1, Table 1). Although not included in the top model, the penalty incurred by including Moonlight intensity does not preclude it from influencing the movements of bobcats.

Coyotes

There was little difference in movements of female ($\bar{x} = 326\,\mathrm{m\,h^{-1}}$, n = 4, SE = 29) and male ($\bar{x} = 337\,\mathrm{m\,h^{-1}}$, n = 6, SE = 48) coyotes. Coyote movements varied seasonally (Fig. 1) (Supplementary material Appendix 1 Table A2), however only the comparison between spring and summer was significant ($t = 6.45$, df = 12 600, $p < 0.001$). Male movements increased more than females from the spring to summer but declined less in winter (Supplementary material Appendix 1 Table A2). Coyotes' movements increased with Moonlight intensity ($t = 3.40$, df = 12 600, $p < 0.001$) (Fig. 2). Coyotes moved farther in the middle of the night than from 17:00 to 22:00 h and from 02:01 to 07:00 h (Fig. 3) (Supplementary material Appendix 1 Table A2), however, these relationships were non-significant. Coyotes moved farther in the night time than in the crepuscular period ($t = -10.62$, df = 12 680, $p < 0.001$) (Fig. 4) (Supplementary material Appendix 1 Table A2), and their movements declined as temperatures increased ($t = -45.66$, df = 12 680, $p < 0.001$) (Fig. 5).

Biological season and its interaction with Night period, Sex, Crepuscularity, Moonlight intensity and Temperature was the model best supported by our data (Model 1, Table 2). Even the removal of the interaction of Biological season with Sex from the model substantially weakened its predictive value (Table 2).

Bobcats versus coyotes

Whereas bobcats' movements seemed to decline from breeding season through summer and then winter, coyotes' movements increased from spring to summer and then declined in winter (Fig. 1) (Supplementary material Appendix 1 Table A1, A2). Bobcats did not display a response to increased Moonlight intensity, whereas coyotes moved farther as Moonlight intensity increased (Fig. 2) (Supplementary material Appendix 1 Table A1, A2).

Bobcats seemed to have bimodal movement patterns declining in the middle if the night, whereas coyote movements peaked in the middle of the night (Fig. 3) (Supplementary material Appendix 1 Table A1, A2). The crepuscular movements of bobcats did not differ from their nighttime movements. However, coyotes moved farther at night than during the crepuscular period (Fig. 4) (Supplementary material Appendix 1 Table A1, A2). Both bobcats and coyotes reduced their movements as temperatures increased (Fig. 5).

The model that best explains the differences between coyotes and bobcats excludes Sex (Model 1, Table 3). However, the inclusion of Sex does not substantially increase the model's AICc score (Table 3). The removal of Moonlight

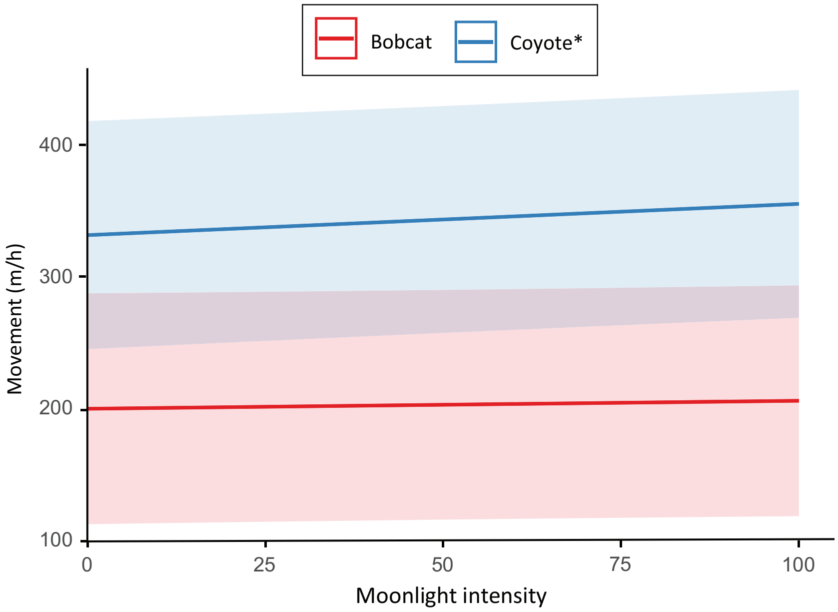

Figure 2. Response of bobcats *Lynx rufus* and coyotes *Canis latrans* to increasing Moonlight intensity from January 2009 to July 2011. *Statistically significant influence of moonlight (Supplementary material Appendix 2 Output A1). Note: Highlighted ribbons represent 95% confidence intervals.

intensity from the model substantially reduces the predictive ability of the model (Table 3).

Discussion

Unsurprisingly, considering their larger home ranges (Melville et al. 2015b) and different hunting styles (Thornton et al. 2004), coyotes' nocturnal movement rates were higher than those of bobcats'. This disparity may be exaggerated by interspecific differences in movement patterns. For example, bobcats in central Texas used less linear routes during nocturnal movements than coyotes (Cooper et al. 2015), and the use of hourly linear displacement as a proxy for movement may underestimate movement distances of bobcats more than those of coyotes.

Bobcats

Longer movement distances of male than of female bobcats is in line with previous studies for bobcats (Bailey 1974, Chamberlain et al. 2003) and other lynx species (e.g. Eurasian lynx, *Lynx lynx*: Sunde et al. 2000, Jedrzejewski et al. 2002) and can probably be explained by female movements being governed by foraging concerns while male movements optimize mating opportunities (Sandell 1989). In the southern United States, bobcats breed between February and May, and rear kittens from June to September (Chamberlain et al. 2003). As in Mississippi (Chamberlain et al. 1998), female bobcats in east Texas moved the shortest distances during

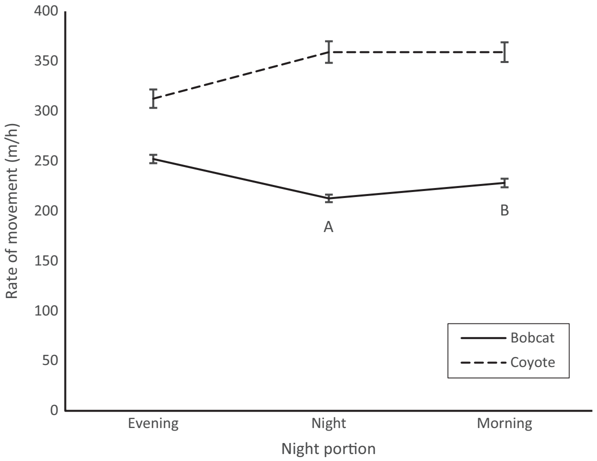

Figure 3. Rates of movement (± 1 SE) by bobcats *Lynx rufus* and coyotes *Canis latrans* relative to night portion in east Texas from January 2009 to July 2011. A and B = Statistically significant influence of night portion (Supplementary material Appendix 2 Output A1).

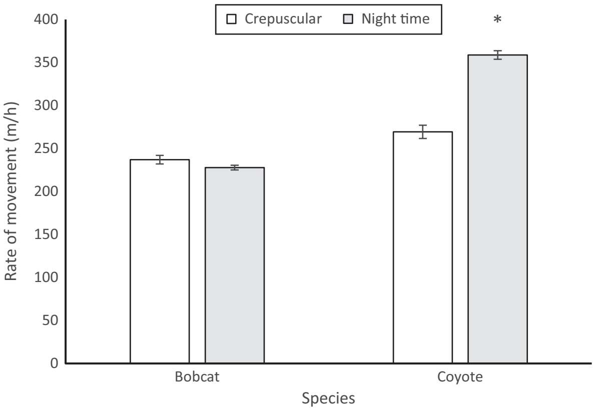

Figure 4. Rates of movement (± 1 SE) by bobcats *Lynx rufus* and coyotes *Canis latrans* relative to crepuscular period in east Texas from January 2009 to July 2011. *Statistically significant difference between night time and crepuscular period (Supplementary material Appendix 2 Output A1).

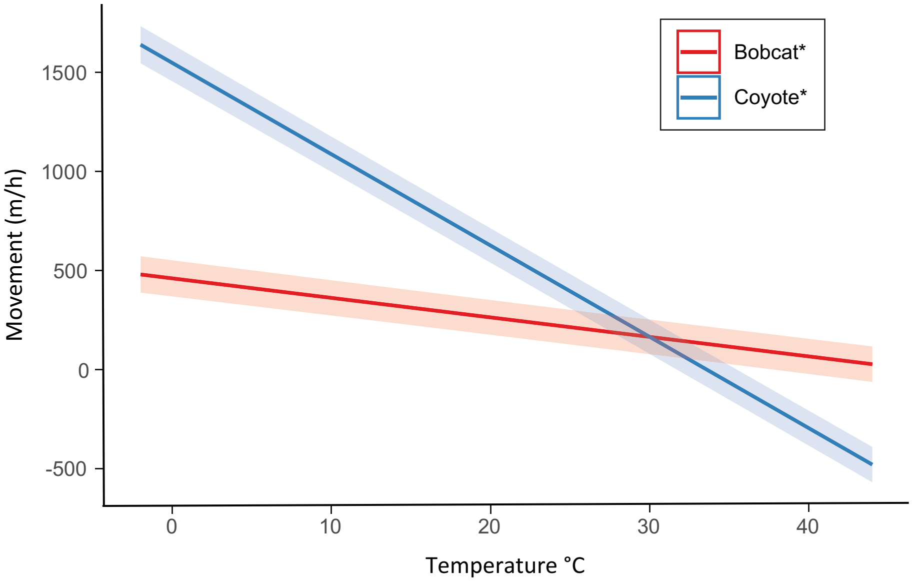

Figure 5. Response of bobcats *Lynx rufus* and coyotes *Canis latrans* to temperature in east Texas from January 2009 to July 2011. *Statistically significant influence of temperature (Supplementary material Appendix 2 Output A1). Note: highlighted ribbons represent 95% confidence intervals.

spring and summer, which may be associated with kitten rearing. Furthermore, this seasonal trend aligns with bobcats' reduced movements at high temperatures (Fig. 5).

Although bobcats are dependent on their sight during hunting (Sunquist and Sunquist 2002, Rockhill et al. 2013), our analysis did not show an increase in bobcat movements as Moonlight intensity increased. This is contrary to Rockhill et al. (2013), who found that bobcats increased their movements at lunar light intensities between 10 and 49%. The lack of response to increasing illumination is surprising, especially as bobcat movements are thought to be inhibited by low levels of illumination (Kavanau 1971, Rockhill et al. 2013). It seems that despite bobcats having poor night vision (Rockhill et al. 2013), bobcat movements in east Texas are not influenced by lunar light.

Like observations elsewhere in the USA (Chamberlain et al. 1998, Tigas et al. 2002, Elizalde-Arellano et al. 2012), bobcat nocturnal movements were bimodal with a clear reduction in movement during the middle of the night. Although generally we found little difference between nocturnal and crepuscular movements for bobcats, this differs from other studies that show bobcats being more active during the crepuscular period than at night (Rockhill et al. 2013, Symmank et al. 2014). It seems that in east Texas, female and male bobcats have different crepuscular activity patterns. Such differential crepuscular activity may have evolved to dampen intraspecific intersexual competition (Rolley and Warde 1985). However, the intrasexual differences in movements between crepuscular and night periods are small and may be of little biological importance.

As in other studies (Zezulak and Schwab 1980, Elizalde-Arellano et al. 2012, Rockhill et al. 2013), our data suggests that temperature is the primary factor influencing bobcat movements in east Texas. It appears that bobcat activity is curtailed at extreme high temperatures (Zezulak and Schwab 1980, Elizalde-Arellano et al. 2012). During winter, when the ambient temperatures are lowest, bobcats move the longest distances. It may be that at low temperatures bobcats need to move farther to satisfy their increased metabolic requirements (Sandell 1989) or to compensate for seasonally lower prey availability.

Coyotes

As has been demonstrated elsewhere (Shivik et al. 1997, McClennen et al. 2001, Elfelt 2014) our data confirm that coyote movements are not influenced by Sex. Our analysis highlights the importance of differential movements between Biological seasons for coyotes in east Texas. In east Texas, as in Mississippi (Chamberlain et al 2000), increased summer movements may be necessitated by provisioning food for pups. Our analysis showed that male and female coyotes in east Texas, like those in the Sierra Nevada (Shivik et al. 1997), increased their nocturnal movements during the summer. This differs from other studies that found that only females travel farther during pup rearing (Holzman et al. 1992, Chamberlain et al. 2000). Their increased summer movement is counterintuitive as high ambient temperature inhibits coyote movements. The relatively short distances travelled by coyotes in spring and winter coincided with pulses of increased resource availability and the pup rearing period. In spring, coyotes use a high proportion of seasonally available fruits (Dumond et al. 2001, Schrecengost et al. 2008, Melville et al. 2015a), this likely reduces the distances that they need to travel to fulfill their metabolic requirements. Winter coincides with the onset of white-tailed deer hunting season (Kilgo et al. 1998). Both research sites were intensively hunted by recreational hunters. Resultant carcass remains, deposited on 'gut piles', provided easily accessible, predictable, localized, seasonal resource nodes during deer hunting season (Crimmins et al. 2012, Gomo et al. 2017).

The increase in movement by coyotes as Moonlight intensity increased is logical as sight is their primary sense for hunting (Kavanau and Ramos 1975). In east Texas, as

Table 1. Model selection for variables thought to influence bobcat *Lynx rufus* movements in east Texas from January 2009 to July 2011.

Model no	Model formulation	Hypothesis	AICc	ΔAICc	R^2	
					Marginal[a]	Conditional[b]
Panel one						
1	Tmp × Sex + Tmp × NQ + Tmp × SB + Tmp × Crep	Tmp and its interaction with all variables except PCM influences the nocturnal movements of bobcats	30667.70	0	0.14	0.38
2	Tmp × Sex + Tmp × NQ + Tmp × SB + Tmp × Crep + Tmp × PCM	Tmp influences the nocturnal movements of bobcats	30669.34	1.65	0.14	0.38
3	SB × Sex + SB × NQ + SB × Crep + SB × Tmp	SB and its interaction with all variables except PCM influences the nocturnal movements of bobcats	30718.83	51.13	0.14	0.36
4	SB × Sex + SB × NQ + SB × Crep + SB × Tmp + SB × PCM	SB influences the nocturnal movements of bobcats	30722.63	54.93	0.14	0.36
5	Sex × NQ + Sex × SB + Sex × Crep + Sex × PCM + Sex × Tmp	Sex influences the nocturnal movements of bobcats	30917.87	250.17	0.14	0.38
6	Sex × NQ + Sex × SB + Sex × Crep + Sex × Tmp	Sex and its interaction with all variables except PCM influences the nocturnal movements of bobcats	30918.88	251.18	0.14	0.38
7	NQ × Sex + NQ × SB + NQ × Crep + NQ × Tmp	NQ influences the nocturnal movements of bobcats	31051.47	383.78	0.13	0.36
8	Crep × Sex + Crep × SB + Crep × NQ + Crep × Tmp	Crep and its interaction with all variables except PCM influences the nocturnal movements of bobcats	31051.59	383.89	0.13	0.35
9	Crep × SX + Crep × SB + Crep × NQ + Crep × PCM + Crep × Tmp	Crep influences nocturnal movements of bobcats	31054.69	386.99	0.13	0.35
10	NQ × Sex + NQ × SB + NQ × Crep + NQ × PCM + NQ × Tmp	NQ influences the nocturnal movements of bobcats	31056.15	388.45	0.13	0.36
11	NQ + SB + Crep + Tmp	Abiotic variables except Sex and PCM influence nocturnal movements of bobcats	31064.20	396.50	0.09	0.35
12	Sex + NQ + SB + Crep + Tmp	Abiotic variables except PCM influence nocturnal movements of bobcats	31064.61	396.91	0.13	0.35
13	Sex + NQ + SB + Crep + PCM + Tmp	All abiotic variables influence nocturnal movements of bobcats (full model)	31066.45	398.75	0.13	0.35
14	PCM × Sex + PCM × SB + PCM × NQ + PCM × Crep + PCM × Tmp	PCM and its interaction with all variables influences nocturnal movements of bobcats	31067.88	400.19	0.13	0.35
15	NQ + SB + Tmp	Abiotic variables apart from Sex, Crep and PCM influence nocturnal movements of bobcats	31067.90	400.20	0.09	0.35
16	PCM × SB + PCM × NQ + PCM × Crep + PCM × Tmp	PCM and its interaction with all variables except for Sex influences nocturnal movements of bobcats	31069.39	401.69	0.09	0.35
Panel two						
A	Tmp × Sex + Tmp × NQ + Tmp × SB + Tmp × Crep	Tmp and its interaction with all variables except for PCM influences the nocturnal movements of bobcats	30667.70	0	0.14	0.38
B	Tmp × Sex + Tmp × NQ + Tmp × SB + Crep	Tmp and its interaction with Sex, NQ and SB, and the inclusion of but no interaction with Crep influences the nocturnal movements of bobcats	30668.29	0.59	0.14	0.38
C	Tmp × Sex + Tmp × NQ + Tmp × SB + Tmp × Crep + Tmp × PCM	Tmp influences the nocturnal movements of bobcats	30669.34	1.65	0.14	0.38
D	Tmp × Sex + Tmp × SB + NQ + Crep	Tmp and its interaction with Sex and SB, and the inclusion of but no interaction with NQ and Cre influences the nocturnal movements of bobcats	30680.45	12.75	0.14	0.38
E	Tmp × NQ + Tmp × SB + Tmp × Crep + Sex	Tmp and its interaction with NQ, SB and Crep, and the inclusion of but no interaction with Sex influences the nocturnal movements of bobcats	30716.90	49.21	0.14	0.37
F	Tmp × Sex + Tmp × SB	Tmp and its interaction with Sex and SB influences the nocturnal movements of bobcats	30897.49	229.79	0.13	0.36
G	Tmp × Sex + Tmp × NQ + Tmp × Crep + SB	Tmp and its interaction with Sex, NQ and Crep, and the inclusion of but no interaction with SB influences the nocturnal movements of bobcats	30960.89	293.19	0.14	0.38

Panel one – models incorporating the full model and the best models for each combination of interacting variables.
Panel two – submodels of the variables interacting with Temperature.
[a] Marginal R^2 is a measure of the variance explained by the fixed effects.
[b] Conditional R^2 is a measure of the variance explained by the whole model (Nakagawa and Schielzeth 2013).
* Interaction of variables.
Tmp = Temperature.
NQ = Night portion.
SB = Biological season.
Crep = Crepuscular period.
PCM = Moonlight intensity.

Table 2. Model selection for variables thought to influence coyote *Canis latrans* movements in east Texas from January 2009 to July 2011.

Model no	Model formulation	Hypothesis	AICc	ΔAICc	R²	
					Marginal[a]	Conditional[b]
Panel one						
1	SB × NQ + SB × Sex + SB × Crep + SB × PCM + SB × Tmp	SB influences the nocturnal movements of coyotes	31954.81	0	0.24	0.34
2	SB × NQ + SB × Crep + SB × Tmp + SB × PCM	SB and its interaction with all variables except Sex influences the nocturnal movements of coyotes	32009.46	54.66	0.24	0.34
3	Tmp × NQ + Tmp × SB + Tmp × Crep + Tmp × PCM	Tmp and its interaction with all variables except Sex influences the nocturnal movements of coyotes	32027.47	72.66	0.24	0.34
4	Tmp × Sex + Tmp × NQ + Tmp × SB + Tmp × Crep + Tmp × PCM	Tmp influences the nocturnal movements of coyotes	32028.71	73.91	0.24	0.33
5	PCM × Sex + PCM × SB + PCM × NQ + PCM × Crep + PCM × Tmp	PCM influences the nocturnal movements of coyotes	32415.46	460.65	0.22	0.32
6	PCM × SB + PCM × NQ + PCM × Crep + PCM × Tmp	PCM and its interaction with all variables except Sex influences the nocturnal movements of coyotes	32415.85	461.05	0.22	0.32
7	Sex × NQ + Sex × SB + Sex × Crep + Sex * PCM + Sex * Tmp	Sex influences the nocturnal movements of coyotes	32425.00	470.19	0.22	0.33
8	NQ × SB + NQ × Crep + NQ × Tmp + NQ × PCM	NQ and its interaction with all variables except Sex influences the nocturnal movements of coyotes	32425.33	470.52	0.22	0.33
9	NQ × Sex + NQ × SB + NQ × Crep + NQ × PCM + NQ × Tmp	NQ influences the nocturnal movements of coyotes	32426.94	472.14	0.22	0.32
10	Crep × SB + Crep × NQ + Crep × Tmp + Crep × PCM	Crep and its interaction with all variables except Sex influences the nocturnal movements of coyotes	32455.88	501.08	0.21	0.33
11	Crep × Sex + Crep × SB + Crep × NQ + Crep × PCM + Crep × Tmp	Crep influences the nocturnal movements of coyotes	32457.61	502.81	0.21	0.32
12	Sex + NQ + SB + Crep + PCM + Tmp	All abiotic variables influence the nocturnal movements of coyotes (full model)	32460.13	505.33	0.21	0.32
13	NQ + SB + Crep + Tmp	Abiotic variables apart from Sex and PCM influences the nocturnal movements of coyotes	32470.74	515.94	0.21	0.33
14	Sex + NQ + SB + Crep + Tmp	Abiotic variables except for PCM influences the nocturnal movements of coyotes	32472.16	517.35	0.21	0.32
15	NQ + SB + Tmp	NQ, SB and Tmp influence the nocturnal movements of coyotes	32483.29	528.48	0.21	0.33
16	Sex × SB + Sex × Crep + Sex × Tmp + Sex + PCM	Sex influences the nocturnal movements of coyotes	32597.30	642.50	0.21	0.32
17	NQ + Tmp	NQ and Tmp influence the nocturnal movements of coyotes	33560.81	1606.01	0.15	0.28
18	Tmp	Tmp alone influences the nocturnal movements of coyotes	33624.09	1669.29	0.15	0.27
Panel two						
A	SB × NQ + SB × Sex + SB × Crep + SB × PCM + SB × Tmp	SB influences the nocturnal movements of coyotes	31954.81	0	0.24	0.34
B	SB × NQ + SB × Crep + SB × PCM + SB × Tmp	SB and its interaction with all variables except Sex influences the nocturnal movements of coyotes	32009.46	54.66	0.24	0.34
C	SB × NQ + Sex + SB × Crep + SB × PCM + SB × Tmp	SB and its interaction with all variables, and the inclusion of but no interaction with Sex influences nocturnal movements of coyotes	32010.67	55.86	0.24	0.33
D	NQ + SB × Crep + SB × PCM + SB × Tmp	SB interaction with Crep, PCM and Tmp, and the inclusion of but no interaction with NQ influences the nocturnal movements of coyotes	32048.73	93.93	0.24	0.33
E	NQ + Sex + SB × Crep + SB × PCM + SB × Tmp	SB interaction with Crep, PCM and Tmp, and the inclusion of but no interaction with NQ or Sex influences the nocturnal movements of coyotes	32049.97	95.16	0.24	0.33
F	NQ + Crep + PCM + SB × Tmp	SB interaction with Tmp, and the inclusion of, but no interaction with NQ, Crep, and PCM influences the nocturnal movements of coyotes	32081.95	127.15	0.24	0.34
G	NQ + Sex + Crep + PCM + SB × Tmp	SB interaction with Tmp, and the inclusion of, but no interaction with NQ, Sex, Crep and PCM influences the nocturnal movements of coyotes	32083.19	128.38	0.24	0.34
H	Crep + NQ + SB × Tmp	SB interaction with Tmp, and the inclusion of, but no interaction with Crep and NQ influence the nocturnal movements of coyotes	32085.93	131.12	0.24	0.34
I	NQ + Sex + SB × Crep + PCM + SB × Tmp	SB interaction with Crep and Tmp, and the inclusion of but no interaction with NQ, Sex and PCM influences the nocturnal movements of coyotes	32086.48	131.67	0.24	0.33
J	NQ + PCM + SB × Tmp	SB interaction with Tmp, and the inclusion of but no interaction with NQ and PCM influences the nocturnal movements of coyotes	32090.97	136.16	0.24	0.34
K	Crep + PCM + SB × Tmp	SB interaction with Tmp, and the inclusion of but no interaction with Crep and PCM influences the nocturnal movements of coyotes	32329.57	374.76	0.22	0.32

Panel one – models incorporating the full model and the best models for each combination of interacting variables.
Panel two – submodels of the variables interacting with Biological Season.
[a] Marginal R² is a measure of the variance explained by the fixed effects.
[b] Conditional R² is a measure of the variance explained by the whole model (Nakagawa and Schielzeth 2013).
* Interaction of variables.
Tmp = Temperature.
NQ = Night portion.
SB = Biological season.
Crep = Crepuscular period.
PCM = Moonlight intensity.

Table 3. Model selection for variables thought to influence both bobcat *Lynx rufus* coyote *Canis latrans* movements in east Texas from January 2009 to July 2011.

Model no	Model formulation	Hypothesis	AICc	ΔAICc	R^2	
					Marginal[a]	Conditional[b]
1	SPP × NQ + SPP × SB + SPP × Crep + SPP × PCM + SPP × Tmp	SPP interaction with all variables except Sex influenced the nocturnal movements of bobcats and coyotes	63188.42	0	0.17	0.34
2	SPP × Sex + SPP × NQ + SPP × SB + SPP × Crep + SPP × PCM + SPP × Tmp	SPP interaction with all variables influenced the nocturnal movements of bobcats and coyotes	63189.98	1.56	0.19	0.34
3	SPP × NQ + SPP × SB + SPP × Crep + SPP × Tmp	SPP interaction with all variables except Sex and PCM influenced the nocturnal movements of bobcats and coyotes	63201.78	13.37	0.17	0.34
4	SPP × NQ + SPP × Crep + SPP × Tmp	SPP interaction with NQ, Crep and Tmp influenced the nocturnal movements of bobcats and coyotes	64654.63	1466.21	0.13	0.30
5	SPP × Crep + SPP × Tmp	SPP interaction with Crep and Tmp influenced the nocturnal movements of bobcats and coyotes	64866.80	1678.38	0.13	0.29
6	SPP × Tmp	SPP interaction with Tmp influenced the nocturnal movements of bobcats and coyotes	64915.23	1726.82	0.12	0.29

[a] Marginal R^2 is a measure of the variance explained by the fixed effects.
[b] Conditional R^2 is a measure of the variance explained by the whole model (Nakagawa and Schielzeth 2013).
* Interaction of variables.
SPP = Species.
Tmp = Temperature.
NQ = Night portion.
SB = Biological season.
Crep = Crepuscular period.
PCM = Moonlight intensity

had been demonstrated for captive individuals (Kavanau and Ramos 1975), coyotes increased their movements as nocturnal light increased. Like coyotes in Arizona (Grinder and Krausman 2001), coyotes in east Texas moved farthest in the middle of the night. This is contrary to the behavior of coyotes in northern Mexico (Arias-Del Razo et al. 2011) where their activity peaked in the mornings and evenings. As in California (Neale and Sacks 2001) and Massachusetts (Way et al. 2004), coyotes in east Texas moved farther during the nocturnal than the crepuscular period. Increased movement after the crepuscular period may be a behavioral response to avoid humans (Chamberlain and Leopold 1999, Kitchen et al. 2000, McClennen et al. 2001, Riley et al. 2003, Wang et al. 2015). It is possible that harvesting of coyotes by humans induces a more nocturnal habit in coyotes in east Texas.

Coyote movements consistently decreased as collar temperature increased. Coyote body temperatures are independent of ambient temperature below ca 25°C but rise steadily above this level. At ambient temperatures >34°C desert coyotes pant, and as temperatures approach 40°C coyotes become stressed (Golightly and Ohmart 1983). Coyotes depend on evaporative cooling to maintain body temperature at high ambient temperatures (Golightly and Ohmart 1983). Unlike the desert environment, where low humidity promotes evaporative cooling, the Pineywoods are hot and humid, especially during summer. These conditions reduce locomotor performance and may cause hyperthermia (Zub et al. 2013). High humidity inhibits evaporative cooling and coyotes may reduce activity to avoid overheating. This may explain coyotes' reduced movements at high perceived temperatures, and why coyote movement peaks in the middle of the night (Fig. 3).

Bobcats versus coyotes

Both bobcat and coyote populations on our study sites were harvested continuously, and consequently, the populations remained at relatively low densities (Davis 2010) throughout the study. Therefore, neither populations are likely to have been resource constrained relative to prey availability (Melville et al. 2015a). Despite this, bobcats tended to move farthest in winter when bobcat diets were least diverse (Melville et al. 2015a), suggesting an increased energy expenditure while hunting. Coyotes, on the other hand, moved farthest in summer when they were provisioning pups and when resource supplements such as fruits and animal remains were not available.

Bobcat night time movements in east Texas were bimodal with reduced movements during the middle of the night, like bobcats elsewhere in the USA (Chamberlain et al. 1998, Tigas et al. 2002, Elizalde-Arellano et al. 2012). Coyotes in east Texas, as in Arizona (Grinder and Krausman 2001), moved farthest in the middle of the night. This could be due to differential nocturnal movement patterns between bobcats and coyotes (Fig. 3), with bobcats reducing their movements when coyotes are most active.

Although activity patterns are governed primarily by nutrition and reproduction (Arias-Del Razo et al. 2011), bobcat and coyote movements are clearly influenced by several abiotic variables. In addition, the responses to these variables cannot be viewed in isolation. The complex interactions of variables that influence bobcat and coyote movements makes it clear that their movements are influenced by mechanisms that are more complex than mere resource availability. For future research, biologists should be cognizant of the complex system of constraints under which bobcats and coyotes operate and ensure that these are incorporated into the development of hypotheses to explain their movements.

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Supplementary material (available online as Appendix wlb-00601 at <www.wildlifebiology.org/appendix/wlb-00601>) Appendix 1–2.