Behavioral adaptations of a large carnivore to human activity in an extremely arid landscape

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Abstract

Driven by the availability of food subsidies and landscape transformation, large carnivore populations are increasingly inhabiting the vicinity of humans. To persist in human proximity, while avoiding conflict and mortality, they must make adjustments in their spatial behavior. Understanding such behavioral adaptations can be crucial to formulate conservation strategies. We used GPS location data to study the movement and space use of protected Arabian wolves in the extremely arid Negev Desert (Israel), where natural prey densities are reduced. We examined wolf preference for the proximity of human infrastructure, while testing the hypothesis that wolves would use areas where ungulates were more likely to occur. Wolves showed a strong spatial association with humans, spending a large proportion of their time in proximity of human infrastructure and moving primarily along roads. Wolves also increased their movement during the night. In addition, wolves that had higher availability of human infrastructure in their home ranges showed increased selection for such features, suggesting a positive functional response. Finally, wolves did not show preference for areas of high ungulate occurrence at either spatial scale. These findings, combined with recent diet analyses, indicate that wolves rely on human subsidies, proportioned by the availability of garbage and agricultural produce. Our results demonstrate that wolves fine-tune their space use to persist in the vicinity of humans. Additional conditions that enable such persistence include effective legal protection and positive local attitudes toward wolves. We conclude that such circumstances can promote spatial coexistence of humans and large carnivores. The strong observed spatial association and evident dietary dependence of wolves on subsidies from a low-density human population may also reflect the conditions that led to dog domestication.

Introduction

Recent human population growth has resulted in the alteration of a large proportion of the planet's landscapes (Newbold *et al.*, 2015). This trend has promoted increasing contact between humans and several animal species, especially wildlife that depend on anthropogenic foods. Large carnivores can directly compete with humans for resources through depredation on livestock (Boitani, 1992; Treves & Karanth, 2003), but can also benefit from relatively abundant and accessible human-derived subsidies such as garbage and carrion (Newsome *et al.*, 2014). Large carnivores can persist at close spatial proximity to humans through behavioral adaptations, such as increased activity during the night (Theuerkauf *et al.*, 2003; Hebblewhite & Merrill, 2008).

Alternatively, these species can spatially avoid encounters with humans using portions of their home range which have lower human activity (Gehrt, Anchor & White, 2009). Despite these behavioral adaptations, in human-altered landscapes, traffic collisions, livestock-related conflict, and harvest are major sources of large carnivore mortality (Treves & Karanth, 2003; Smith *et al.*, 2010). Thus, large carnivores that live in the vicinity of human infrastructure are faced with a trade-off between increased access to resources and higher mortality risk as a consequence of conflict (Woodroffe, 1998). Favorable attitudes and effective protection may mitigate such conflict and enable large carnivores to persist in the vicinity of humans (Chapron *et al.*, 2014; Carter & Linnell, 2016). Because of worldwide large carnivore population declines (Ripple *et al.*, 2014), it is important to

understand the conditions under which viable large carnivore populations persist in human vicinity.

The diet and feeding habits of gray wolves *Canis lupus* have repeatedly promoted conflict with humans (Boitani, 1992), resulting in the species' extirpation from most of its historical range (Musiani & Paquet, 2004; Ripple *et al.*, 2014). Wolf movement and behavioral responses to human activity vary according to their diet, the type and intensity of human activities. Where wolves spatially avoid residential areas, their densities in human proximity can decrease (Hebblewhite *et al.*, 2005; Kittle *et al.*, 2015). Conversely, in boreal areas, wolves can increase their use of forest clearings and roads, a behavioral strategy that elevates their probability of encountering prey (Whittington, Clair & Mercer, 2005; Lesmerises, Dussault & St-Laurent, 2012). Thus, wolves inhabit areas with a wide variety of human densities (Theuerkauf, 2009) and, under certain ecological conditions, may persist in the vicinity of humans (Hefner & Geffen, 1999; Newsome *et al.*, 2017), as is the case in the European continent (Chapron *et al.*, 2014). Identifying the behavioral strategies that enable wolf persistence could assist in the conservation of this and additional canid species living near human habitation by informing management strategies aimed at mitigating conflict (Treves & Karanth, 2003).

To assess the circumstances that promote the persistence of wolves in human proximity, we studied a population of Arabian wolves *C. lupus arabs* inhabiting the arid Negev Desert. Past scat analyses via wolf scat revealed the predominant items in Arabian wolf diets to be cow carrion, fruit, and human garbage (Shalmon, 1986), suggesting that these wolves may rely on human subsidies (Hefner & Geffen, 1999). We hypothesized that one reason wolves can maintain relatively high densities in this arid landscape is by adjusting their behavior to gain increased feeding opportunities in the presence of anthropogenic infrastructure. To evaluate this hypothesis, we established three predictions, and tested them using GPS location data from wolves occurring across a gradient of human land use.

Spatial and temporal adjustments to anthropogenic activity may make it possible for large carnivores to persist in landscapes where encounters with humans would increase the likelihood of conflict and mortality (Hebblewhite & Merrill, 2008; Theuerkauf, 2009). In addition to human subsidies, the Negev ecosystem contains a number of ungulate populations that persist in low densities. We therefore predicted that, similar to wolves in boreal ecosystems (Nelson *et al.*, 2012; Kittle *et al.*, 2015), Arabian wolves would select for areas with higher probability of encountering native ungulate prey. Because the occurrence of ungulates coincided with areas of limited human infrastructure, our alternative prediction was that wolves would select for spatial proximity of anthropogenic features such as settlements, agricultural fields and garbage deposits, and show preferential movement along dirt roads. We predicted that this pattern would especially be significant during night time, when human activity and surrounding temperatures are diminished (Theuerkauf *et al.*, 2003).

Our third prediction further examined the importance of habitat in close proximity to human infrastructure to wolves by testing for a functional response in habitat selection to human infrastructure. Functional responses in habitat selection occur when selection changes as the availability of a landscape feature changes (Mysterud & Ims, 1998; Mason & Fortin, 2017). For example, a resource might be strongly selected where it is rare, but used as available or avoided where it is common, suggesting that the resource may be limiting or of high importance to an animal (Roever, van Aarde & Leggett, 2012). Thus, we predicted that wolves that have higher availability of anthropogenic features in portions of their home range would show increased selection for these features (Houle *et al.*, 2010), or that wolves with few high-quality human-derived food patches within their home range would show increased selection for these patches.

Materials and methods

Research area

This study was conducted in the arid (mean monthly temperatures range: 15–32°C; mean yearly precipitation range: 28.7–195.1 mm) Negev desert. The study area extended from Lehavim (31.374°N, 34.817°E) in the north to Eilat (29.558°N, 34.952°E) in the south, mostly within the borders of Israel (Fig. 1). Its western and central portions include several mountain ridges, crossed by dry gorges and wide washes. The eastern portion, a part of the Rift Valley, presents a savanna-like habitat characterized by shrubs and *Acacia sp.* trees. Settlements in the Rift Valley area (total population – 6000), arranged along the main road to Eilat, subsist mostly from agriculture and tourism (Sagie *et al.*, 2013). Most human activity in the mountain areas is concentrated around military bases (Fig. 1), surrounded by fences which deter human entrance but permit wildlife passage.

Arabian wolves are the largest carnivore in the Negev ecosystem. Potential ungulate prey populations in the area include the dorcas gazelle *Gazella dorcas*, estimated at 1200–1500 (density: 0.04–$0.05/km^2$), onager *Equus hemionus*, estimated at 200, and Nubian ibex *capra nubiana*, at 500–1000 individuals (density: 0.02–$0.04/km^2$; A. Tsoar, *unpublished data*). Such low density of prey cannot sustain the estimated size of the area's wolf population (approximately 100 individuals; Cohen, Barocas & Geffen, 2013). Estimates of wolf dietary consumption (Metz *et al.*, 2012) suggest that, to sustain a population of 100 wolves, minimum available ungulate biomass (at a conservative 2 kg/wolf/day for Arabian wolves) must be 73 000 kg/year. The maximum estimated ungulate biomass (Smith *et al.*, 2003) in the study area is 126 500 kg. Thus, a diet based solely on natural prey would be unsustainable for this wolf population.

Animal capture

We conducted captures in locations where wolves were previously observed, while taking safety and logistical constraints into consideration. Capture locations varied with respect to their proximity to human infrastructure (Fig. S1). We captured wolves using daily monitored Victor #3
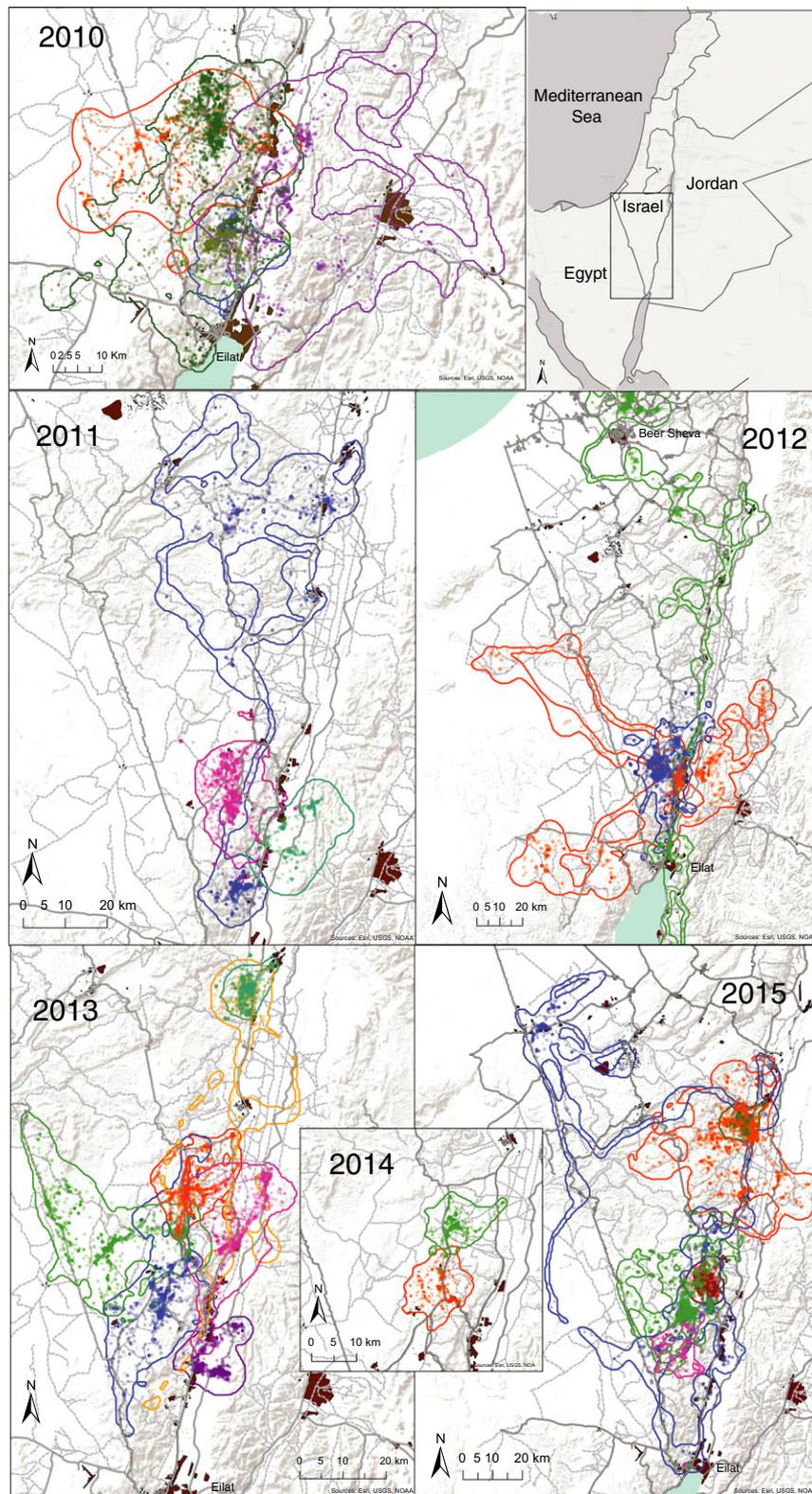
Figure 1 Map of Arabian wolf research area in southern Israel, including portions of Egypt and Jordan. Colored contours represent individual home ranges. Semi-transparent dots represent GPS locations, brown-colored polygons denote areas of human activity, continuous gray lines represent paved roads, and dotted lines represent dirt roads. GPS locations from 28 Arabian wolves were collected in 2010–2015. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

softcatch leg-hold traps (Woodstream co., Lititz, PA, USA). During daylight periods, traps remained covered. We immobilized captured wolves with a Dormitor-Ketamine hydrochloride mix at a dose of 10 mg/kg body weight. Trapping and handling procedures were conducted according to permit # 2017/41568 issued by the Israel Nature and Parks Authority (INPA). We fit adult wolves with eartags and Followit (Lindesberg, Sweden) 1C Light GPS collars (weight: 222 g), with UHF and GSM download and remote drop-off. We programmed GPS collars to record one fix during daytime hours and hourly fixes during twilight and night time (5 PM to 5AM), following previously observed periods of wolf activity (Hefner & Geffen, 1999).

Habitat covariates and home range estimation

Human activity in the study area is characterized by small settlements, agricultural infrastructure (e.g., storage silos), diverse crop fields and date orchards, military bases, and garbage dumps (Sagie *et al.*, 2013). To assess the influence of these features on wolf space use and movement, we developed GIS layers quantifying distance from anthropogenic features, and distance from paved and dirt roads. We did not separately quantify distance from residential areas, agriculture, dumps, and military bases because during preliminary analyses, we found that these distances were highly correlated and because not all features were present within all wolf home ranges. To quantify the probability of encountering ungulate prey, we developed a layer based on 10 750 observations of the dorcas gazelle (the most abundant prey species in our study area), made between 2008 and 2016.

We derived a kernel density function, using an optimized smoothing factor based on standard distance and median distance for each pixel (Silverman, 1986; Fig. S2). In addition, to quantify elevational and topographical variation within wolf habitats, we developed layers describing elevation, slope, aspect, and topographic position (Table 1).

Wolf movement is characterized by distinct behavioral modes, which are detectable using movement speeds and turning angles (Gurarie *et al.*, 2011). The dynamic Brownian Bridge movement model (bBBMM; Kranstauber *et al.*, 2012) accounts for such heterogeneous movement and is therefore suitable for wolf GPS fix datasets. We used dBBMM to calculate each individual's home range area during the period when it was tracked, and subsequently delineated 99% utilization density contours (Fig. 1). We used these home ranges as the spatial scale for assessing wolf space use.

Resource selection functions

We assessed the natural and anthropogenic landscape variables that potentially predict wolf space use using Resource Selection Functions (RSF; Manly *et al.*, 2002). Within each individual's home range (third order selection; Johnson, 1980), we generated random points (available) that matched the number of GPS locations (used), and extracted habitat covariates for each used and available point. We tested all pairs of predictor variables for collinearity using Spearman's r, and found low collinearity (all $r < 0.46$). We subsequently built a full model that included all habitat covariates (Table 1). We then ran eight models in which individual variables were removed and a null model with no fixed effects (Table S1). We used mixed-effects logistic regression

Table 1 Description and sources of spatial variables used as predictors of Arabian wolf space use and movement using resource selection functions (RSF) and step selection functions (SSF)

Name	Description	Range	Source	RSF	SSF
Human distance	Euclidean distance (km) from human features, including settlements, agricultural features, garbage dumps, and military bases	0: 40	INPA, satellite images of Jordan, Egypt	+	+
Main road distance	Euclidean distance (km) from paved roads	0: 31	INPA, satellite images of Jordan, Egypt	+	
Dirt road distance	Euclidean distance (km) from dirt roads	0: 15	INPA, satellite images of Jordan, Egypt	+	
Main road presence	Presence within 500 m buffer distance from paved roads	0: 1	INPA, satellite images of Jordan, Egypt		+
Dirt road presence	Presence within 500 m buffer distance from dirt roads	0: 1	INPA, satellite images of Jordan, Egypt		+
Gazelle	Point Density Kernel of 10 750 gazelle observations during 2008–2016.	0: 10	INPA	+	+
Elevation	Value of a Digital Elevation Model (DEM) for each cell	−400: 1680	Aster GDEM, asterweb.jpl.nasa.gov/gdem.asp	+	+
Slope	Rate of elevation change among cells in degrees	0: 65	Developed from DEM	+	+
Aspect	The downslope direction of the maximum rate of change in value from each cell to its neighbors	−1: 1	Developed from DEM	+	+
TPI	Topographic position index – calculated as the difference between the elevation of a cell and the mean elevation of its neighboring cells. Negative values represent valley bottoms.	−53: 44	Developed from DEM	+	+

to parametrize models. We observed significant overlap between adjacent wolf home ranges (Fig. 1) but did not detect any pair of individuals moving together, confirming previous findings (Hefner & Geffen, 1999). Thus, we did not add a pack-related level to our random effects (Hebblewhite & Merrill, 2008). Because we suspected that wolves would show individual variation in space use (Hebblewhite & Merrill, 2008), we specified a random intercept and random slopes for all variables in each examined model, following recommendations by Gillies *et al.* (2006).

We tested the full model for multicollinearity using variance inflation factors (VIF; Zuur, Ieno & Elphick, 2010). We assessed relative support for the full model compared to the additional models, including all factors except one, using Akaike Information Criteria (AIC; Burnham & Anderson, 2002). To validate our full RSF model, we performed k-folds cross-validation for RSFs with five bins (Houle *et al.*, 2010). To account for possible bias as a result of spatio-temporal overlap in wolf home ranges, we performed the same analysis fitting the full model with a dataset including only individuals that did not have overlapping home ranges (Fig. 1; n = 21). We also performed a similar procedure with the dataset excluding dispersing individuals. Results were the same between models parameterized using both data subsets (Table S2, S3, S4), thus we report results from the full dataset. All analyses were performed in the R computational environment (version 3.1.0; R Development Core Team 2011).

Movement analysis

To assess whether wolves exhibited temporal avoidance of human activity, we classified locations as twilight or night based on daily sunrise and sunset times. We considered the straight-line distances travelled by wolves between hourly fixes as steps. We used a linear mixed model to examine if location time period (twilight or night) was a good predictor of step length (log-transformed for normality), with wolf ID specified as a random intercept. In addition, we used the Wilcoxon signed-rank test to assess the periods of time wolves were active by comparing the proportion of steps in which individual wolves showed limited movement (shorter than 100 m) among twilight and night locations.

To investigate the factors that influenced wolf movement at the patch level (fourth order; Johnson, 1980) and how movement varied among periods of different human activity, we used step selection functions (SSF; Fortin *et al.*, 2005) separately for the twilight and night datasets. To examine true movement, we censored all steps shorter than 50 m, accounting for telemetry error and periods in which there was limited movement. We used a matched case–control design, generating 20 available steps, each starting from the same point as the observed step. We based the length and angle of available steps on the observed distribution of step lengths and turning angles of the individual's matching sampled observed steps. For each observed or available step, we extracted habitat covariates at the end point of each step (Thurfjell, Ciuti & Boyce, 2014). After testing all pairs of

variables for collinearity, we fit a full model, including distance from human features, presence/absence within 500 m of main and dirt roads, elevation, slope, aspect, and topographic position (Table 1). The model was parametrized using conditional logistic regression with each stratum identified as a used point and its 20 paired available points. We calculated robust SE and 95% CI of parameters using generalized estimating equations (GEE; Craiu, Duchesne & Fortin, 2008). Because data was continuous for all wolves and rarely spanned over 160 days (Table S5), clusters in the GEE were defined by individual. This resulted in 28 clusters. To test for a functional response of wolves (Mysterud & Ims, 1998) to the availability of human features, paved roads and dirt roads, we added an interaction term to the full model for each of these features, providing an indication for how selection for these features changes with respect to the amount of these features available (calculated as the mean covariate value of the available points for each stratum) for each step. We compared the fit of the full model with models including functional responses using quasi-likelihood information criteria (QIC; Pan, 2001). We validated the robustness of SSFs using five folds cross-validation repeated 100 times, following the framework developed by Fortin *et al.* (2009) for SSFs. In brief, this cross-validation method is intended for a case–control design, where the SSF is built using a randomly selected 80% of the data and it is used to estimate predicted values of the withheld 20% of data. Using the predicted values, the observed location of each stratum is ranked against its associated available steps (from 1 to 11, i.e., the observed step and its paired 10 available steps). Ranks of observed steps are tallied into 11 bins, and a Spearman rank correlation (r_s) is employed to test whether the highest ranked bins include the most number of observed steps. We also assessed the mean range of expected r_s (i.e., a random choice of points) based on the above methods, but instead of ranking the observed step against the 11 possible, we randomly selected 1 of the 10 available steps for each stratum (Fortin *et al.*, 2009).

Results

Between 2010 and 2015, we captured 28 wolves, including 22 males and 6 females, and collected a total of 44 002 locations. Wolves were tracked for periods of 15–344 days (mean ± SE = 132.5 ± 10.9 days). Unusually long movements and detection of several distinct core use areas indicated that four wolves were tracked during dispersal movement (Fig. 1). For remaining territorial individuals, the mean home range area (±SE) calculated by dBBMM during the tracking period was 664.9 ± 115.6 km^2 (Table S5).

All RSF variable VIF scores were less than 3, suggesting negligible multicollinearity. The best predictor of wolf space use at the home range level was distance to human infrastructure, showing a negative relationship, indicating selection for locations that were closer to human features compared to random (β ± SE = –0.26 ± 0.06; Fig. 2, Table S2). Of the eight examined variables, removal of distance to human infrastructure resulted in the most significant change in AIC support
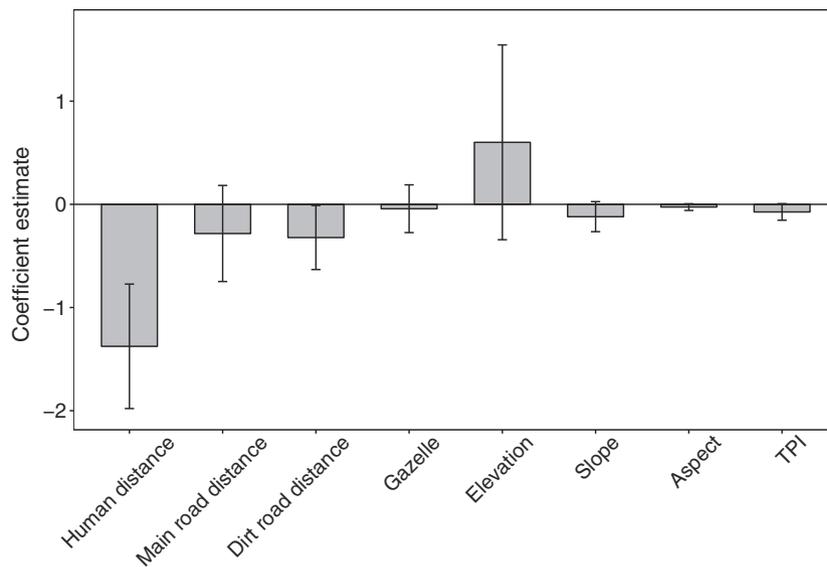
Figure 2 Plots of full model coefficient estimates from a mixed effects resource selection function (RSF) fit to Arabian wolf space use data. Standardized coefficients (gray bars) and 95% confidence intervals are shown for each factor. Variables are further described in Table 1. RSF was fit to GPS locations from 28 Arabian wolves, collected in 2010–2015.

compared to the full model (ΔAIC = 15.1; Table S1); 61.1% of wolf locations were inside or within 2 km of human infrastructure, and 27.6% of locations were in the range between 2 and 5 km (Fig. S3). Wolves also selected areas closer to dirt roads ($\beta \pm$ SE = –0.22 $\pm$ 0.11; Fig 3), valley bottoms (TPI covariate $\beta \pm$ SE = –0.01 $\pm$ 0.01; Fig. 3), and flatter areas (aspect covariate $\beta \pm$ SE = –0.05 $\pm$ 0.03). Removing gazelle occurrence probability had a small effect on AIC compared to the full model (ΔAIC = 1.9), suggesting wolf space use was not driven by the probability of encountering a gazelle (Table S2, S3). Cross-validation of the full model indicated good predictive ability (mean $r \pm$ SE = 0.84 $\pm$ 0.03).

We recorded 10 855 GPS fixes (25%) during twilight and daytime and 33 147 fixes during night time (75%). The length of twilight period during which wolves were tracked was, on average, 1.13 h (2.2 mean twilight locations per individual per day). Wolves showed limited movement between daytime fixes and their first twilight locations (mean $\pm$ SD = 0.74 $\pm$ 0.07 km). Wolf hourly step lengths were on average almost twice the length during night time (mean night step length $\pm$ SD = 1.32 $\pm$ 0.01 km) than during twilight (mean twilight step length $\pm$ SD = 0.77 $\pm$ 0.02 km) and time period was a strong predictor of step length (mixed model $\beta \pm$ SE = 0.27 $\pm$ 0.04; $P < 0.001$). The proportion of steps equal to or shorter than 100 m, indicating limited movement, was higher during twilight (0.50) compared to at night (0.30). This pattern was confirmed by the Wilcoxon signed-rank test ($W = 106$, $P < 0.001$). In addition, we observed differences in the distribution of step lengths, with higher skewness toward short step lengths during twilight (skewness = 2.15) compared to night (skewness = 1.71; Fig. S4).

At the patch scale, wolves moved into proximity to human infrastructure and moved toward gentler slopes both at twilight

and at night (Table S6; Fig. 4). In addition, the SSFs that included a functional response to anthropogenic features outperformed competing models (night: ΔQIC = 558.8; twilight: ΔQIC = 16.9, Table S7). Wolf movement in the proximity of paved and dirt roads was higher at night, indicating that they used these linear features for travel. The SSF coefficient of terrain position was negative at night ($\beta = -0.004$), indicating movement toward valley bottoms. The observed patterns of increased proximity to roads and lower terrain positions were not evident for twilight steps (Table S6). Cross-validation results indicated good fit of both the twilight and night model with the human proximity functional response term (twilight $r_s = 0.65 \pm 0.11$, random = 0.02 $\pm$ 0.22; night $r_s = 0.84 \pm 0.04$, random = 0.05 $\pm$ 0.23).

Discussion

Here, we demonstrate that Arabian wolf presence within or in the vicinity of anthropogenic features (89% of locations inside or within 5 km of human infrastructure) is evident at multiple scales, and proximity to anthropogenic features is the strongest predictor of wolf space use. These patterns were especially evident given that human infrastructure only occurs over 2% of the research area landscape (Fig. 1, Table S5). Our results confirm initial findings for this population (Hefner & Geffen, 1999) and provide support for the prediction that wolves select for spatial proximity of anthropogenic features. According to the best-supported SSF model, wolves in areas with higher availability of human infrastructure showed increased selection for these features. These findings are in line with evidence that wolves inhabiting the vicinity of human residential and agricultural areas make behavioral adjustments (Hebblewhite & Merrill, 2008; Theuerkauf, 2009). During night, wolves showed increased
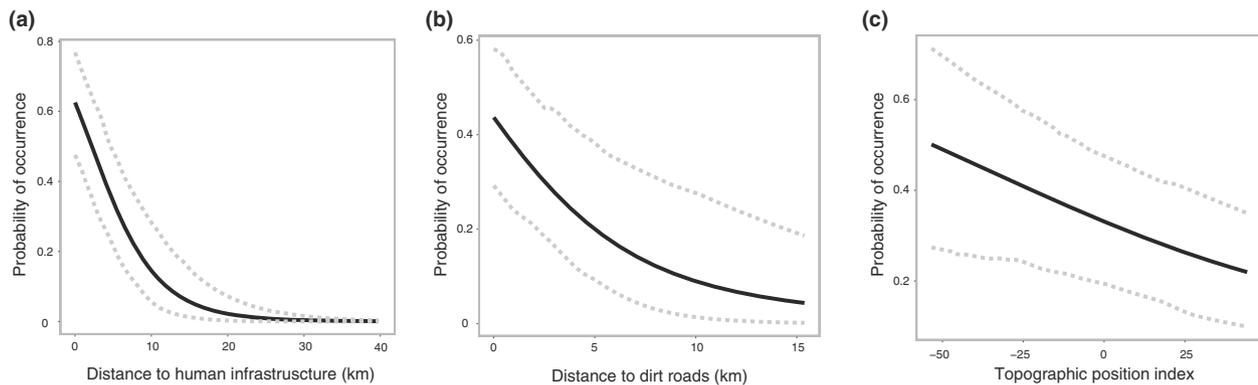
Figure 3 Plots of significant fixed effects from a mixed effects resource selection function (RSF) fit to Arabian wolf space use data. Means (black lines) and 95% confidence intervals (dotted lines) were obtained by non-parametric bootstrapping with 100 repeats for each predicted fixed effect value, while keeping all other variables fixed at the mean. RSF was fit to GPS locations from 28 Arabian wolves, collected in 2010–2015.

movement compared to twilight and limited daytime fixes, a pattern that could result from high daytime temperatures or temporal avoidance of human activity (Hefner & Geffen, 1999).

Evidence suggests that, in systems with ecologically relevant ungulate abundances, wolf resource selection is primarily driven by prey distribution or native prey habitat suitability (Nelson *et al.*, 2012; Kittle *et al.*, 2015). In contrast, in the Negev study area, ungulate prey resources were scarce and wolves did not show selection for areas where gazelles occurred more frequently, failing to show support for the prey habitat prediction. The Dorcas gazelle is the most abundant prey species in the Negev and for which the best occurrence data are available. However, because we did not have comparable data on other potential prey species or the direct consumption of prey by wolves, dorcas gazelle occurrence may provide an incomplete estimate of prey availability in our study area. While exploiting anthropogenic features, wolf movement was consistent with a positive functional response to human features (Mason & Fortin, 2017). This pattern, more evident at night but also during twilight time, suggests that human infrastructure provides resources which are important for the persistence of this wolf population. These findings differ from studies of wolves in boreal ecosystems, which showed greater avoidance of human features when these were more abundant in their territory (Houle *et al.*, 2010). Taken together, the lack of support for the prey habitat hypothesis, our findings of strong selection for proximity of anthropogenic features, and past findings on wolf diet, suggest that Negev wolves mostly rely on human subsidies (e.g., garbage and agricultural produce) and could not persist at present densities based on native prey alone (Hefner & Geffen, 1999).

Consistent with previous findings on wolves which forage in anthropogenically modified areas (Boitani, 1992) and specifically on this population (Hefner & Geffen, 1999), we did not observe marked wolves moving in groups larger than 2–3 individuals. Contrary to gray wolves which consistently hunt for large prey (MacNulty *et al.*, 2012; Metz *et al.*,

2012), ours and previous findings suggest that Arabian wolves in southern Israel mostly depend on human subsidies. In addition to affecting wolf space use and movement, this dietary preference may have implications for the wolf social system, resulting in smaller group sizes. The observed territorial overlap among several pairs of tracked individuals also suggests that the abundance and predictability of food patches near human habitation may also influence the configuration of wolf territories. Further investigations of spatial overlap and avoidance between wolves in this system and the social implications of this population's dependence on human subsidies are warranted.

Arabian wolves moved along both paved and dirt roads during night. The research area contains an intricate network of dirt roads, with low traffic volumes, mainly used for agriculture, military training and recreational activities. Movement along paved roads during night contradicted evidence from other systems (Ciucci, Masi & Boitani, 2003; Whittington *et al.*, 2005). Asphalt roads are sparse in southern Israel (Fig. 1) and low human densities in the area result in relatively limited traffic volume (the majority of Negev roads show less than 5000 vehicles/day; Israel Statistics Bureau). Therefore, especially during night, paved roads could be functionally analogous to dirt roads and facilitate wolf movement. Roads in the Negev may enable movement among anthropogenic resource patches and increase the chances of exploiting these food sources for wolves. Our findings indicate that space use in the vicinity of human-made linear features may facilitate movement and minimize energy expenditure (Zimmermann *et al.*, 2014), providing wolves with benefits which outweigh mortality risks associated with roads. Our findings that Arabian wolves were more active and moved along roads during night, a pattern not evident during twilight, may additionally be explained by the need to reduce on energy expenditure by avoiding activity in elevated daytime temperatures, characteristic of the arid environment.

Our results document an Arabian wolf population which persists with high spatial association with human activity and relies on human subsidies – conditions which may have
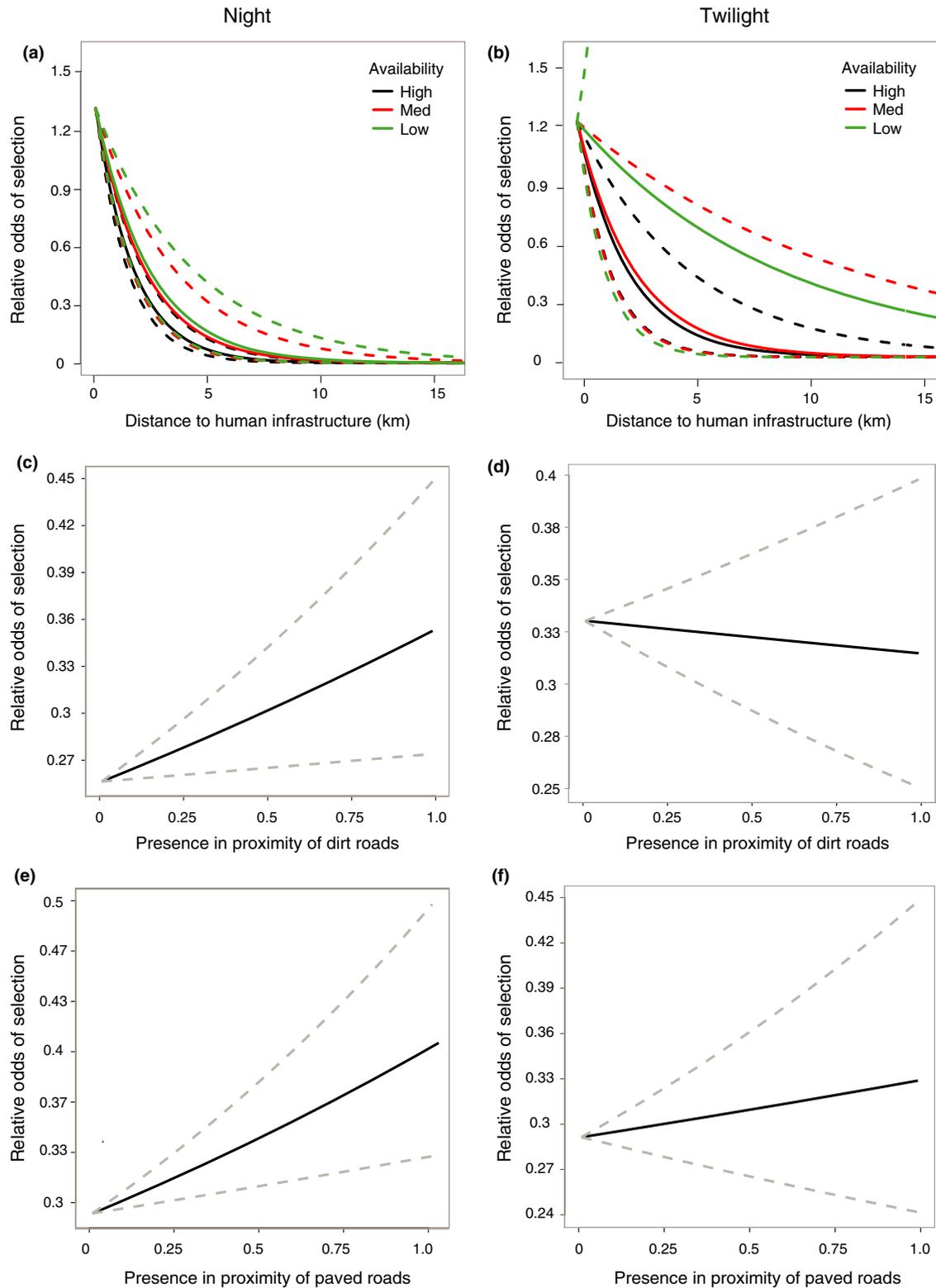
Figure 4 Relative odds (exponent [exp] of selection coefficient) of selection as a function of distance to human infrastructure (a, d), presence in proximity of dirt roads (b, e), and presence in proximity of paved roads (c, f) during night and twilight hours for Arabian wolves in southern Israel, 2010-2015. Full lines represent predicted relationships using mean selection coefficients, with dotted lines representing the 95% CI of the prediction. For the functional response plot (a), three different levels of availability of human features were calculated by 5%, 50% and 95% quantiles. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

facilitated dog domestication. Evidence suggests that the genetic signatures of European and Middle Eastern gray wolves are strongly present in modern dog breeds (Larson *et al.*, 2012). Our study area's rural, low-density human population may reflect the conditions prevalent when dog domestication took place (Clutton-Brock, 1995). Furthermore, because of low availability of ungulate prey compared to human subsidies, wolves that were less afraid of human proximity may have become reliant on human-derived foods for their subsistence (Driscoll, Macdonald & O'Brien, 2009; Newsome *et al.*, 2017). Thus, the conditions of our study area and the observed behavior of Negev wolves may provide a glimpse into one of the routes to dog domestication.

Both sociological adaptations of humans and behavioral adaptations of large carnivores are necessary to enable the persistence of these species in human proximity (Musiani & Paquet, 2004; Chapron *et al.*, 2014). Arabian wolves remain legally protected and positively regarded by local inhabitants in our study area (Cohen *et al.*, 2013), likely as a consequence of their ability to avoid conflict with humans and the small role of livestock growing in local economic activities. Wolves in other parts of the Middle East, where livestock and chickens have more economical significance, are not as favorably regarded by human populations, leading to frequent conflict (Reichmann & Saltz, 2005; Tourani *et al.*, 2014). Our results, combined with recent population estimates (Cohen *et al.*, 2013), suggest that under certain ecological conditions, large canid populations can persist in close proximity of human habitation by fine-tuning their movement, feeding habits, and activity budgets. These behavioral patterns support the notion that anthropogenic landscapes may be driving evolutionary processes by affecting the movement and behavior of commensal species, especially carnivores (Newsome *et al.*, 2017).

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Listing of fixed effects and selected model selection rankings for several random-slopes resource selection functions (RSF) fit to Arabian wolf GPS location data in southern Israel, 2010–2015.

Table S2. Coefficients (β), standard errors (SE), z scores and 95% confidence intervals of fixed effects and variance of random slopes of the full model resource selection function (RSF) for home-range scale wolf space use. Variables are further described in Table 1. Data included GPS locations from 28 Arabian wolves in Southern Israel, collected in 2010–2015.

Table S3. Coefficients (β), standard errors (SE) and 95% confidence intervals of fixed effects and variance of random slopes for full model RSF for home-range scale wolf space use. Variables are further described in Table 1. Data included GPS locations from 21 Arabian wolves which did not show overlap in their home ranges in southern Israel, collected in 2010–2015.

Table S4. Coefficients (β), standard errors (SE) and 95% confidence intervals of fixed effects and variance of random slopes for full model RSF for home-range scale wolf space use. Variables are further described in Table 1. Data included GPS locations from 23 Arabian wolves which were not dispersing during the tracking period in southern Israel, collected in 2010–2015.

Table S5. Listing of all individual Arabian wolves, sex, tracking period, home range sizes and density of human features within home ranges. Wolves were captured and tracked in the Negev desert, southern Israel, in 2010–2015.

Table S6. Coefficients (β), robust standard errors (SE) and significance of parameterized step selection functions (SSF) modeling wolf movement during day and night for full datasets. Output of the night SSF includes an interaction term describing functional response to human distance. Variables are further described in Table 1. Data includes GPS locations from 28 Arabian wolves in Southern Israel, collected in 2010–2015.

Table S7. Listing of model selection results for several step selection functions (SSF), divided by twilight and night locations, with the full dataset. Model fit was assessed using quasi-likelihood information criteria. SSFs were built from GPS location data from 28 Arabian wolves in southern Israel, 2010–2015.

Figure S1. Map of Arabian wolf *(Canis lupus arabs)* capture locations in southern Israel. Wolves were captured using foothold traps and fit with GPS collars between 2010 and 2015.

Figure S2. Map of of dorcas gazelle *(Gazella dorcas)* occurrence probability in southern Israel and neighboring areas, derived from a density kernel of 10,750 observations made during 2008–2016. Gazelle probability of occurrence was used as a predictor in models of Arabian wolf resource selection and step selection.

Figure S3. Histogram of the proportions of wolf locations at increasing distances from human infrastructure. Data was summarized from 28 Arabian wolf locations, collected in southern Israel in 2010-2015.

Figure S4. Histogram of wolf step length frequencies during twilight and night time. Data was summarized from 28 Arabian wolf locations, collected in southern Israel in 2010–2015.