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ORIGINAL PAPER

Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features

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Abstract In wolves, most offspring mortality occurs within the first 6–8 months of their life. As wolf pups pass this entire period at either the den or rendezvous sites, their selection by wolf packs may affect pup survival and recruitment. Rendezvous sites are important for pup survival as they are used during summer and early autumn, when intense human activity may increase pup mortality. Adult wolves and pups can be killed by livestock guarding dogs during summer and intentionally or accidentally during large game hunting in autumn. This study describes factors related to rendezvous site selection in order to enhance their protection and management. We studied the rendezvous site selection of 30 wolf packs in central and northern Greece between 1998 and 2010, after locating 35 sites using the simulated howling survey method and telemetry. We considered a series of environmental and anthropogenic predictors of wolf rendezvous site selection at two spatial scales. At the landscape-population scale, wolves selected rendezvous sites below 1,200 m asl, with large inter-site distance (mean, 12.9 km), and avoided partially forested or open habitats, indicating preference for covered, spaced areas with seasonally stable resources. At the home range scale, wolves selected rendezvous sites away from forest roads and villages, close to water sources, and in areas with low forest fragmentation, indicating avoidance of human presence and disturbance. In the summer of 2011, we used an ensuing resource selection model (RSF, AUC=0.818) to successfully locate seven new rendezvous sites outside our previous survey area, verifying the utility of prediction maps (all new sites were at areas with 0.8–1 model probability). Rendezvous prediction maps can be used to reduce field effort when monitoring wolf populations, assess livestock predation risk, design protected areas, and reduce human disturbance on reproductive wolf packs.

Keywords Wolf · Homesite · Rendezvous site · Human activity · Forest fragmentation · Prediction maps

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Introduction

Successful reproduction and pup survival are critical demographic components related to wolf population dynamics and species recovery (Boitani 2000; Fuller et al. 2003). Many studies identified resource availability as the main factor determining wolf reproductive success (e.g., Fuller 1989b; Fuller et al. 2003), while others showed wolf human-caused mortality to be an important inhibitor of wolf reproduction and population recovery (e.g., Liberg et al. 2012). Homesite selection by wolf packs can be closely related to both these factors. It can directly influence access to food resources by reproductive wolf packs (Frame et al. 2008) as well as disturbance of nurturing adults and pups from humans (Frame et al. 2007; Argue et al. 2008; Habib and Kumar 2007; Nonaka 2011). The highest risk of pup mortality occurs during the first 6 months of their age (Fuller et al. 2003) when still occupying homesites (i.e., dens and rendezvous sites). Dens are heavily used during spring for parturition and after birth of pups, while rendezvous sites are selected during summer and early autumn after den abandonment in early summer (Packard 2003). During this entire pup rearing period, the breeding pair and other pack members move continuously to and from dens and rendezvous sites in order to feed and protect the offspring (Alfredeen 2006; Ruprecht et al. 2012). In Greece, the period of rendezvous site use coincides with increased human activities, such as widespread grazing of livestock accompanied by guarding dogs and the onset of wild boar (*Sus scrofa*) hunting. The increased wolf movements and human presence in this period results in higher encounter frequency between wolf packs and livestock guarding dogs and/or hunters and, as a consequence, a high rate of wolf pup mortality (Iliopoulos 1998, 1999, 2000; Iliopoulos and Petridou 2012). Excessive human disturbance close or inside to homesites may also lead to their abandonment and the translocation of pups (Person and Ingle 1995; Weaver et al. 1996; Frame et al. 2007; Habib and Kumar 2007; Argue et al. 2008).

During environmental impact assessments (EIAs) or the development of management plans for large construction (e.g., highways) or resource extraction (e.g., mining, timber harvest) projects, it is important that local wolf dens and rendezvous sites are identified so as to minimize the activities' impact on local wolf populations (e.g., Paquet and Darimont 2002; Lesmerises et al. 2013). In Greece, the typically short period of field surveys afforded to EIAs for such projects means that wolf homesite detection may be incomplete. Moreover, stochastic events such as wolf pack breeder loss which may cease wolf reproduction for some years in an area (Brainerd et al. 2008) may hinder homesite detection during field surveys. The ability to predict the location of wolf homesites using environmental and anthropogenic parameters would help address such problems, contributing to the improved development of wolf-sensitive action timetables. Moreover, such prediction models would be particularly useful in identifying priority sites for wolf conservation initiatives, assessing livestock predation risk (Gula 2008; Treves et al. 2011), and improving the efficiency of wolf population monitoring schemes over large areas (Ausband et al. 2010; Stenglein et al. 2010).

While dens are especially important for pups, in human modified landscapes rendezvous sites may play an equally important role in wolf pup survival (Paquet and Darimont 2002; Fritts et al. 1995). Recent research has shown topographic landscape features, vegetation structure and habitat type, presence of water, human disturbance, and protection status of an area to be good predictors of wolf rendezvous site (e.g., Norris et al. 2002; Theuerkauf et al. 2003; Capitani et al. 2006; Person and Russell 2009; Unger et al. 2009; Ausband et al. 2010; Kaartinen et al. 2010). Until now, in Europe, rendezvous site selection has been studied only in Poland (Theuerkauf et al. 2003) and Italy (Capitani et al. 2006). To fill this gap in Greece, we examined between 1998 and 2010 the rendezvous site selection patterns of thirty wolf packs—a large proportion of the estimated 100 packs in the country (Iliopoulos 2009). The analysis aims to identify the most important landscape attributes, resource availability variables, and anthropogenic landscape features affecting rendezvous site selection at the (a) landscape-population and (b) home range scale. Additionally, we test the hypothesis that wolves select rendezvous sites primarily in areas where pups will be safer from human-caused mortality, predicting that distance from roads, human settlements, and less fragmented forest landscapes would be positively related to rendezvous site selection. Finally, we examine the robustness of the home range resource selection model and its implications for management purposes, using a posteriori original field data.

Materials and methods

Study area

Surveys for locating wolf rendezvous site occurred in two regions in central and northern Greece covering a total area of 6,700 km^2 (Fig. 1). The a posteriori test of the generated rendezvous site predictive model was conducted at three small "out of sample" areas with a total surface of 300 km^2 (Fig. 1). Across all these areas, elevation ranges from 100 to 2,500 m and temperature from −20 to 38 °C. Evergreen oak (*Quercus coccifera*) scrublands dominate areas up to 700 m elevation, deciduous oak (*Quercus* sp.) forests are abundant between 600 and 1,100 m, conifer forests of fir (*Abies borisii regis*) and black pine (*Pinus nigra*) above 1,000 m, and beech (*Fagus sylvatica*)–fir mixed forests the 1,000–1,800 m zone. Scrublands and forests cover 65 % of the study area, with remaining being natural grasslands and agricultural or mixed agricultural–forest areas. Average human population density, excluding cities, is 15 inhabitants/km^2 (data for 1999: Ministry of Interior). Village density ranges from 0.6 to 5.4 settlements/100 km^2. Livestock grazing is practiced throughout the study area, and shepherd dogs are widely used for livestock protection from large carnivores (i.e., wolf and brown bear *Ursus arctos*). The 100–500 m elevation zone is primarily used as wintering area of nomadic livestock flocks from October to May; these flocks are moved to the 1,200–2,400 m elevation zone. At the 500–1,000 m zone, grazing is practiced by residing free-ranging livestock flocks year-round. Average density of sheep and goats is 67.21, cattle 2.55, and free-ranging pigs 2.9 heads/km^2. The forest road network is extensive, with a mean density of 2.43±0.63 km/km^2. Hunting for birds and mammals lasts 6 months, beginning from August 20 and is practiced with trained hunting dogs for birds and hare (*Lepus europaeus*) and also with drive hunts for wild boar. Hunting is prohibited inside the Northern Pindos National Park,

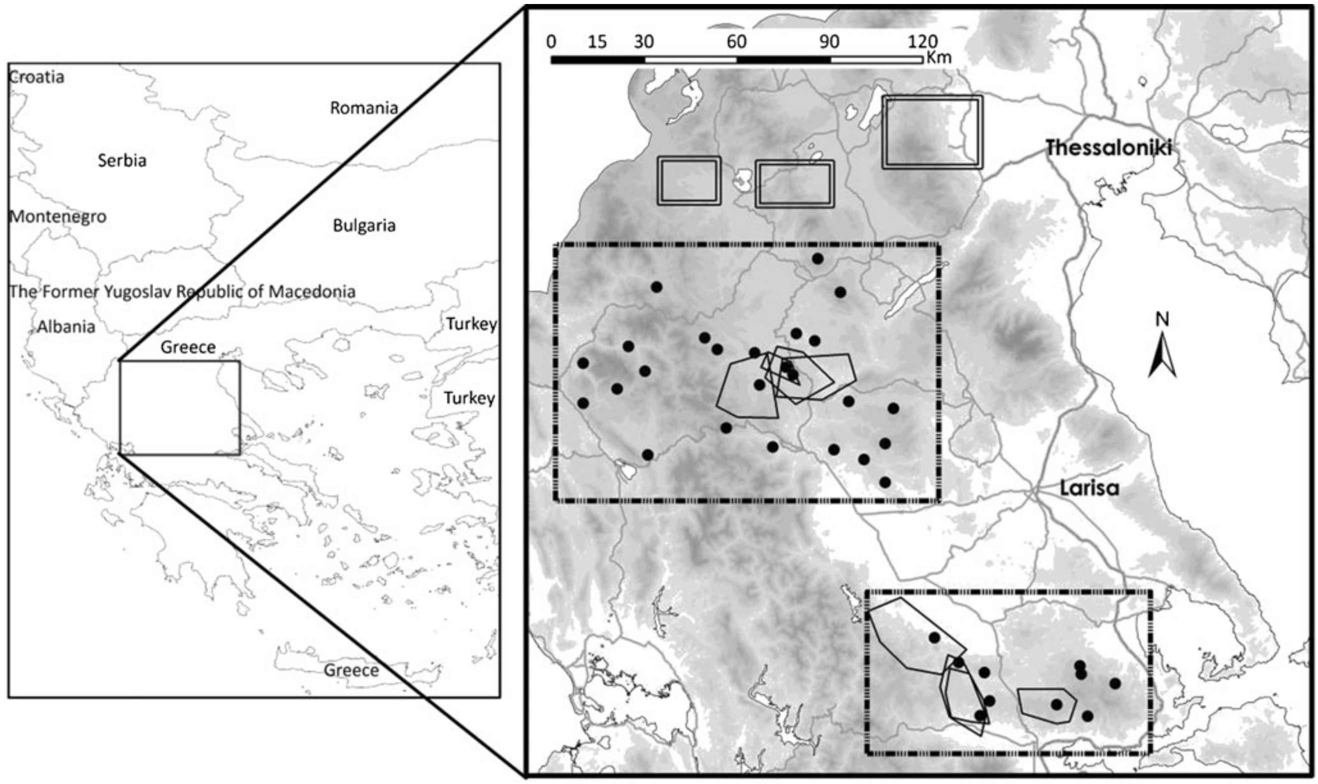


Fig. 1 Map of the study areas showing a) main sampling areas (*dashed polygons*, 6,700 km^2) monitored during 1998 and 2010 to locate rendezvous sites used for analysis and creation of a resource selection model and b) "out of sample" areas (*double line polygons*, 300 km^2) monitored during summer of 2011, which were used to check the robustness of the RSF model. *Solid line polygons* indicate home ranges (minimum convex polygons) of radio-collared packs studied between 1998 and 2011. *Black dots* represent rendezvous sites (n=35) of 30 different wolf packs that were used for modeling rendezvous site selection

Vikos-Aoos National Park core areas, and 47 smaller reserves covering in total 12 % of the study area.

Rendezvous site surveying

Surveying for wolf rendezvous site took place between 1998 and 2010, and the ensuing model was tested in the field in 2011. Six out of the 30 packs were tracked using satellite and radio-telemetry, permitting direct investigation of putative rendezvous sites. Each year between July and September, rendezvous site surveying and confirmation was carried out by the "simulated howling survey method" in a saturated census (Harrington and Mech 1982). This time is preferred as the wolf packs are still sedentary (Packard 2003), the distinction of pup howls from those of adults is feasible (Harrington and Asa 2003), and the response rate is high (Harrington and Mech 1982). We applied the method in all 30 pack areas, where and when recent field data confirmed wolf presence, so as to minimize false-absence records, a common problem in used versus unused studies (Boyce et al. 2002). Field evidence included tracks of two or more wolves, markings, direct sightings of wolves or wolf pups, livestock damage reports, and records from camera traps. When a wolf pack response was elicited, the azimuth of the howl(s) was recorded and the distance to responding wolves estimated during daylight revisits. A site (n=35) was classified as a rendezvous site based on presence of pups when (a) a wolf pup response was heard at least twice during the same summer period (n=29 sites) and (b) only adult wolves were heard but pup presence was verified by other field evidence, such as captured or dead pups, direct sightings, and images of pups from camera traps (n=6 sites). To distinguish among located neighboring rendezvous sites, we repeated the simulated howling protocol during the same night. Nevertheless, in all cases, inter distance was longer than the threshold of 5 km suggested by Capitani et al. (2006) or 6.4 km by Ausband et al. (2010).

We included a rendezvous site in the analysis only once, even if it had been reused by a pack over multiple years. For each rendezvous site (n=35), we randomly selected a non-overlapping unused site (Hawth's tools 3.7 for ArcGIS 211 9.3), at distances ≤5 km, in order to minimize the probability to be located outside of the respective wolf pack home range. Both used and unused sites were considered as circular surfaces, with a radius of 800 m (area of 2 km^2), as average size of known rendezvous sites from collared wolf packs during this study was 2.2±0.39 km^2 (n=8 wolves). “Unused” sites located over lakes, heavily disturbed areas, and purely agricultural or open habitat areas were excluded from all analyses.

Data analysis

We initially analyzed the selection of rendezvous sites at the landscape-population scale (second order selection; Johnson 1980) by comparing the use of rendezvous sites versus the availability of three major variables in the study area: (a) livestock summer density (June-October) in three classes: 0–32, 33–79, and >80 heads/km^2; (b) elevation zones in four classes: 100–500, 501–800, 801–1,200, and 1,201–2,500 m, classified with the quantile method (ArcGis 9.3, ESRI); and (c) Corine landuse types grouped in six classes: evergreen scrublands, deciduous forests, conifer forests, transitional scrubland to forest, mixed agricultural–forest habitats, and natural grasslands. It was not possible to include more variables in the analysis, as detailed spatial data at this scale were lacking. We determined the selection ratio (SR) for each variable class (units=1 km^2) as follows (Manly et al. 2002):

$$W_i = o_i/\pi_i$$

where o_i is the proportion of the ith class sampled inside rendezvous sites and π_i is the proportion within the study area. W_i >1 indicates preference, while W_i <1 indicates avoidance of the i class. We calculated Bonferroni-corrected confidence intervals (Manly et al. 2002) as follows:

$$W_i \pm Z_{\alpha}/(21)\mathrm{SE}(W_i)$$

where 1 is the number of classes per variable, α=0.1, and SE is the standard error of W_i. The SE(W_i) equation takes into account variation in resource selection from all different rendezvous sites (Rogers and White 2007). If confidence intervals overlap with 1, i class is used according to availability.

We then analyzed rendezvous site selection at the home range scale (third order selection; Johnson 1980) by comparing rendezvous and unused sites with multivariate logistic regression (Hosmer and Lemeshow 1989; Capitani et al. 2006; Ausband et al. 2010). For each rendezvous and control site pair, we measured habitat and landscape characteristics (Table 1) at a resolution of 10×10 m, using Aster satellite images, DTM military maps, and Corine landuse maps in ArcGis 9.3 (ESRI). Forest roads and active farms were mapped in the field. Livestock density was spatially adjusted according to the actual location of active farms. Perennial water sources were mapped from military maps of 1:50,000 scale (Hellenic Geographical Military Service). Forest fragmentation indices were estimated with Patch Analyst 4 (Rob

Table 1 Variables describing anthropogenic, resource availability, landscape, and habitat attributes that were used as candidate covariates in logistic regression analysis at the home range scale to examine selection patterns of wolf rendezvous sites (n=35) by wolf packs (n=30) during 1998–2010 in the main study area

Human settlements and infrastructure
Distance from center of site to nearest village (m): class 1 (1,000–2,120 m), class 2 (2,121–2,880 m), class 3 (>2,880 m) (quantile classification)
Forest road length inside site (m)
Distance from center of site to nearest forest road (m)
Distance from center of site to nearest active farm (m)
Distance from center of site to nearest protected area (m)
Water presence
Perennial stream length inside sites (m)
Distance from center of site to nearest water source (m)
Vegetation structure and form
% Forest cover
% High visibility forest–scrubland
% Mature forest
% Young scrubland–forest
% Nonforested area
% Mixed forest
% Deciduous forest
% Evergreen forest
Shannon diversity index for Corine landuse types
Topographic characteristics
Altitude: range (m) and median (m)
% Flat
% North
% East
% South
% West
Aspect: Shannon diversity index
Slope (degrees): average and SD
Visibility from site periphery: sum of values
Cumulative solar radiation of site (days from 200 to 300): average
Hillshade: average, SD, and sum of values
Profile curvature: average, SD, and sum of values
Forest fragmentation indexes
NUMP—number of forest fragments
MPI—mean proximity index
TE—total edge (m)
ED—edge density
AWMSI—area weighted mean patch fractal dimension
TCA—total core area
CAD—core area density
MCA—mean core area
TCAI—total core area index
Livestock density
Average sheep density at site (head per km^2)
Average goat density at site (head per km^2)
Average cattle density at site (head per km^2)
Average pig density at site (head per km^2)

Rempel, Centre for Northern Forest Ecosystem Research, Canada) for ArcView3.2 (ESRI). We regrouped Corine landuse maps to describe vegetation form, independent of habitat type. Categorical covariates entered models as "dummy" variables.

We conducted analysis including all variables in a full model and sequentially removed covariates with lowest b/SE ratio, until variable reduction ceased to improve the model performance (Arnold 2010). Selected covariates were further combined to create candidate models. Variables correlated at Pearson's $r>|0.5|$ were tested separately. We selected as best model the most parsimonious, statistically significant model (Hosmer and Lemeshow χ^2 test), with the largest R^2 Nagelkerke, R^2 Cox and Snell values (Boyce et al. 2002) and overall percent of correct classification of RS. For each variable i included in the model, we estimated the R_i statistic (Field 2005) which describes the relative importance of each variable with the following formula:

$$R_i = \sqrt{\frac{\frac{b_i}{\mathrm{SE}_i} - 2df_i}{-2\mathrm{LL}}}$$

where b_i is the slope of variable i, SE_i is the standard error of b_i, df the degrees of freedom of i, and LL is the log likelihood.

Performance was evaluated with integration of area under curve (AUC) after the calculation of the ROC (receiver operating characteristic curve) according to (Boyce et al. (2002). All statistical analyses were performed with SPSS 13 (SPSS Inc, Chicago, USA).

For a preliminary, out of sample, testing of model robustness, we calculated rendezvous site suitability at three smaller new areas of 300 km^2 (Fig. 1). We created a grid surface covering the test areas with a cell size of 70×70 m. We then created raster surfaces with the same extent and cell size to visualize ecogeographical variables that entered the final logistic regression model (see Table 4). Variable raster surfaces had a buffer zone of 1,000 m around the study area boundaries so as to account for no-data values during calculations. At each cell, we assigned a unique value derived by each variable raster surface. An 800-m-radius moving window (FRAGSTATS 4.1, McGarigal et al. 2002) was used to estimate forest fragmentation covariate values for each grid cell considered in the final model (TCAI index). We calculated the probability of each reference grid cell constituting the center of a rendezvous site using the logistic regression equation derived from the final model. Thus, each cell of the test study areas was assigned a probability value ranging from 0 to 1. To produce the final suitability rendezvous site maps, we rerun the moving window procedure at a radius of 800 m (corresponded to a rendezvous site of 2 km^2 in size) around each grid cell in order to smooth the probability maps by averaging probability values of neighboring cells included at that specific radius. Calculated rendezvous site suitability ranged accordingly from 0 to 1. We then reclassified probability with the equal interval method that creates classes within an equal probability range of 0.1 to produce prediction maps with ten suitability zones (Fig. 2). All analyses were performed using ArcGiS 9.3 (ESRI).

During the summer 2011, we carried out a saturated census to locate rendezvous sites currently occupied or/and used during the last 2–3 years as to increase sample size of rendezvous sites after verifying previous use when possible. We initially undertook a preliminary field assessment census during July 2011 to define areas where wolf packs were present. During this assessment, we mapped all available direct and indirect information indicating presence of wolf packs, such as spatially localized wolf signs (scats, tracks, markings, diggings), and cross referenced information on wolf group howling and pup sightings provided by local shepherds and hunters. During August and September 2011, we undertook a saturated simulated howling survey (Harrington and Mech 1982) in the three new study areas where current wolf presence was mapped during preliminary census. We used the same two evaluation criteria for classification of sites as rendezvous ones, when wolf howling was heard as previously described. When a wolf response was not elicited at a site but other strong indications of wolf reproduction were evident (e.g., farmer reports on pup sighting, howling and presence of dens), we visited—if possible—the sites for identification of field signs suggesting use by wolf pups. Field surveys were conducted independently from GIS model interpretation.

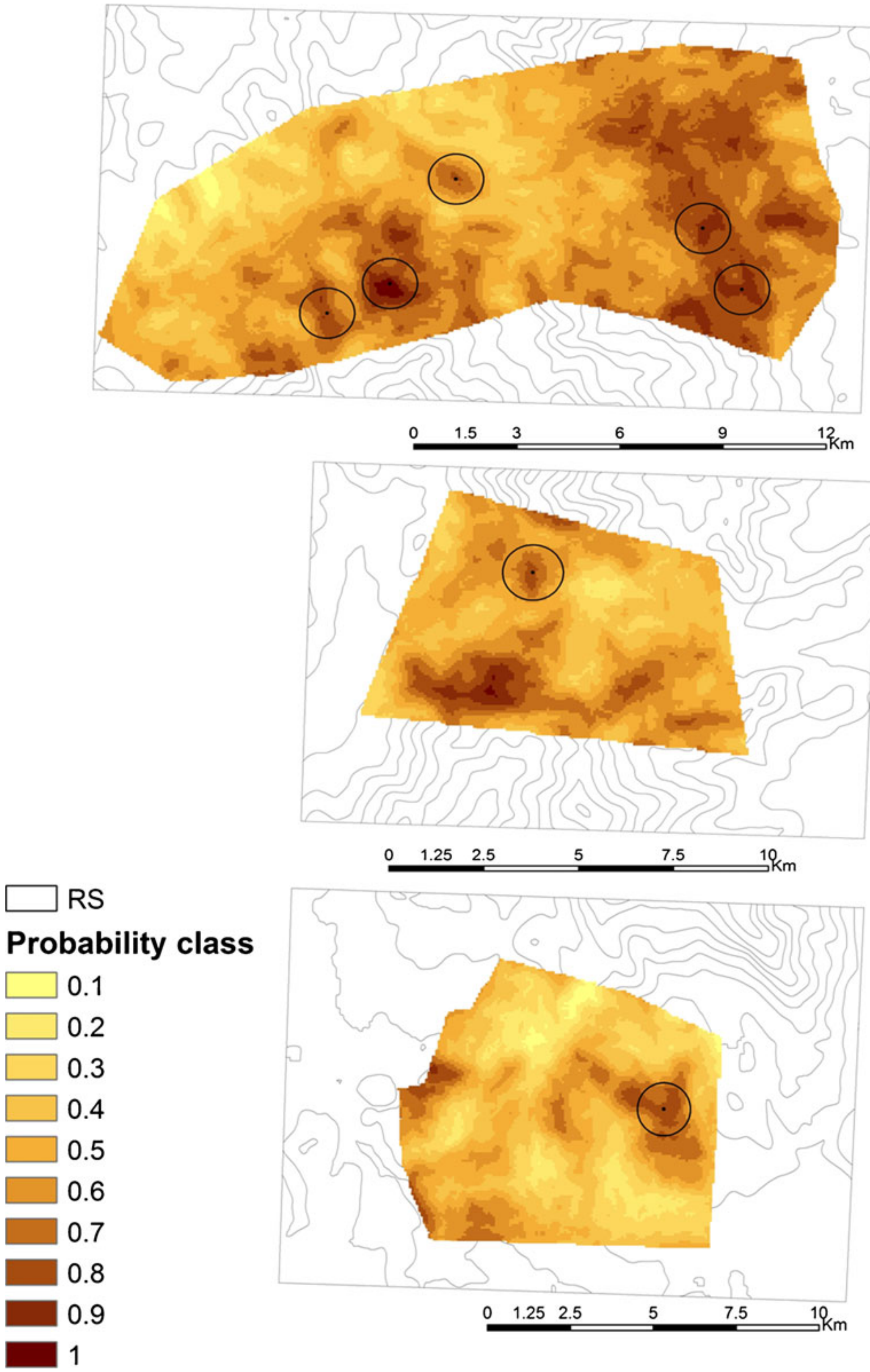
We calculated percent of use of each suitability class i, inside new RS and the percent of standardized selection ratio B_i derived from w_i as follows:

$$\%B_i = 100\frac{w_i}{\sum_1^{10} w_i}$$

Results

During the 1998–2010 survey, we identified a total of 35 rendezvous sites belonging to the 30 different wolf packs studied. We were able to monitor reuse pattern in ten of these rendezvous sites, belonging to nine more intensively studied packs, by checking if those were repeatedly occupied by adult wolves and pups. Checks were performed with the same protocol for at least two different summers per site (range=2–6) but not necessarily during consecutive years. Use and reuse history of these ten rendezvous sites is presented in Table 2. Seven of these ten rendezvous sites incorporated also an active

Fig. 2 Rendezvous site prediction map (70×70m grid cell size) in the three "out of sample" test study areas monitored in summer of 2011, after application of the home range-scale logistic regression equation, derived from resource selection analysis of 35 rendezvous sites used by 30 wolf packs in the main study area. Probability classes (n=10) were created with the equal-probability interval method. Closed circles of 800 m radius (2 km^2) represent new rendezvous sites (n=7) used by four wolf packs, while *black dots* represent their center. All new rendezvous sites located in the field had their center in high suitability areas (0.8–1) and their overall average suitability was 0.736±0.096 (SD)



den inside or at a relatively close distance (<2 km). Dens were located with the use of telemetry data and presence of wolf pups verified with simulated howling in six cases and camera trap pictures in one case. Average inter-rendezvous site distance between different wolf packs was 12.9±1.7 km (range=10.7–16.6 km, n=12 pairs) and did not significantly differ between sub-portions of the study area (Kruskal–Wallis test, H=2.682, df=3, exact P=0.509, n=4).

At the landscape-population scale, wolves did not select any livestock density zone but avoided establishing rendezvous sites at altitudes >1,200 m and mixed agricultural–forest habitat or grasslands. There was a nonsignificant tendency for

Table 2 Use and reuse history of ten rendezvous sites occupied by the nine, more intensively studied, wolf packs that were monitored for two to six different years in the main study area during 1998–2011

Wolf Pack	Years monitored	Years of use (years of monitoring)	Comments
1	1999, 2011	2 (2)	Reuse after 12 years
2	2006, 2010	2 (2)	Reuse after 4 years
3	2006, 2011	2 (2)	Reuse after 5 years
4	2006, 2010, 2011	1 (3)	
5 (RS1)	2002–2007	5 (6)	Reused annually—stopped after breeder loss
5 (RS2)	2002–2007	5 (6)	
6	2008, 2009	1 (2)	
7	1999, 2000	2 (2)	
8	1999, 2003	2 (2)	Reuse after 4 years
9	1998–2000	3 (3)	Reused annually for 3 consecutive years

selecting the 501–800 m zone and the evergreen scrubland zone (see Table 3).

At the third order selection (home range scale), four variables entered the final model (Table 4). Wolves selected rendezvous sites farther from forest roads (P=0.007, mean±SD=435±326 m, range=73–1614 m), closer to a permanent water source (P=0.012, mean±SD=500±434 m, range=0–1,707 m), in less fragmented forested areas (P=0.040), and farther from villages (P=0.019, mean±SD=2,819±1,234 m, range=1,047–6,026 m). The model correctly predicted 80 % of rendezvous sites and according to the estimated AUC value (0.818, SE=0.051) can be considered a "useful application" (see Boyce et al. 2002).

In summer 2011, we identified seven new rendezvous sites of 2 km^2 area each in the "out of sample" study areas (Fig. 2). Although total surface of the "out of sample" evaluation areas was small (300 km^2), the rendezvous sites were spaced at large distances apart from each other (>10.2 km). Identified rendezvous sites corresponded to four different wolf packs. Five of these seven sites where currently occupied by wolves during the 2011 field census and successfully located with the simulated howling survey method (Fig. 2).

Table 3 Selection ratios w_i, standard errors, and Bonferroni corrected confidence intervals (CCI) per w_i, for each habitat (n=6), altitudinal (n=4), and livestock density (n=3) classes, considering selection of rendezvous sites (n=35) by wolf packs (n=30) versus their availability at the main study area during 1998–2010, at the landscape-population scale (<1 indicates avoidance and >1 indicates selection of a particular class; ns indicates use according to availability)

	Bonferroni CCI				
	w_i	SE (w_i)	Lower	Upper	Significance
Habitat type					
Evergreen scrubland	1.38	0.31	0.63	2.13	ns
Deciduous forest	1.27	0.31	0.52	2.03	ns
Conifers	1.22	0.36	0.36	2.07	ns
Transitional scrubland	0.79	0.22	0.27	1.31	ns
Natural grassland	0.57	0.17	0.15	0.99	<1
Agricultural–forest	0.52	0.16	0.14	0.90	<1
Altitudinal zone					
0–500 m	0.86	0.20	0.41	1.31	ns
501–800 m	1.37	0.23	0.87	1.88	ns
801–1200 m	1.26	0.28	0.63	1.88	ns
>1,201 m	0.20	0.1	−0.02	0.43	<1
Summer livestock density zone					
0–32 head/km^2	0.95	0.21	0.49	1.40	ns
33–79 head/km^2	1.09	0.22	0.63	1.55	ns
>80 head/km^2	0.96	0.24	0.47	1.47	ns

Table 4 Results from the best logistic regression model [model χ^2 (Hosmer and Lemeshow test)=2.758, df=8, P=0.949; R^2 (Cox and Shell)=0.304; R^2 (Nagerkelke)=0.405] describing selection of rendezvous sites (n=35) by wolf packs (n=30) at the home range scale in the main study area during 1998–2010. Apart from b coefficients, R statistic was calculated to describe the relative importance of each variable to the model

Covariates	Coefficient b	SE	R	P	Odds ratio	95.0 % CI	
						Lower	Upper
Distance from forest roads (m)	0.004	0.001	0.232	0.007	1.004	1.001	1.006
Distance from water (m)	−0.002	0.001	−0.209	0.012	0.998	0.997	1.000
Total core area index (TCAI)	0.060	0.027	0.172	0.040	1.062	1.007	1.121
Distance from nearest village (Class 3)	1.372	0.668	0.151	0.019	3.945	1.066	1.601
Constant	−4.829	2.057	0.190	0.008			

One of the sites was occupied by wolves the previous year (2010). Its actual use by a wolf pack was verified after inspection of many diggings, spatially concentrated food remains still present in the area, and/or other objects carried by wolves. Moreover, a wolf den was demonstrated in the field by a local shepherd, 1.4 km away from the rendezvous site, who had discovered the den and seen the pups in early June 2010. Although we did not find any signs of current wolf activity in the seventh rendezvous site, there were cross-referenced reports related to pup rearing from several farmers in adjacent areas, who characterized the site as a "traditional" wolf homesite. Indications of rendezvous use included wolf group howling and many wolf pup sightings during summers between 2007 and 2009. Relevant information was considered adequately sufficient as to finally include also this site in the analyses.

All new rendezvous sites were located in high-suitability classes (mean±SD=0.736±0.096, range=0.6–0.86), as derived from probability prediction maps (Fig. 2). The predominant probability class was the 0.8, while standardized percent selection ratios (%B_i) were highly correlated to suitability levels (r_s=0.988, P<0.01, Fig. 3). All rendezvous sites had their centers in areas with estimated probability >0.8, which totally covered 9.9 % of the "out of sample" study areas.

Discussion

Our analyses of rendezvous site selection produced some interesting results that have been recorded for the first time in Greece. At the population-landscape scale, wolves avoided altitudes >1,200 m, while there was a nonsignificant tendency to prefer the medium altitude zone (501–800 m) to establish rendezvous sites. In Greece, high altitudes (>1,200 m) are characterized by more food sources, but this is highly seasonal and food abundance peaks only during summer. On the other hand, lower altitudes (<1,200 m), and especially the 501–800 m zone, are characterized by less fluctuation in food sources, as

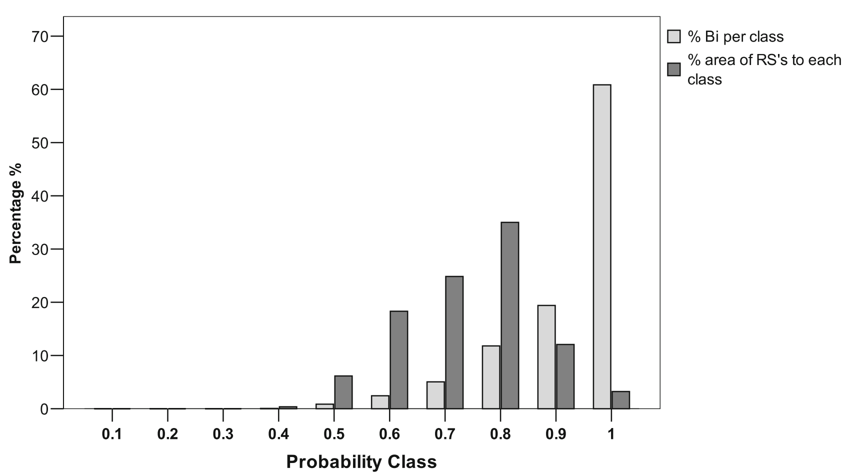


Fig. 3 Percentage distribution (*dark gray bars*) of the total surface of the new rendezvous sites (n=7) located in the "out of sample areas" at each probability class, after assigning predicted probability values to each rendezvous site cell (70×70m) derived from rendezvous site probability prediction maps, and standardized %B_i values (*light gray bars*). B_i is the standardized value (range, 0–100 %) of each probability class selection ratio w_i inside the new rendezvous sites (see "Materials and methods" for equation used)

livestock, currently the main wolf prey in Greece (Papageorgiou et al. 1994; Migli et al. 2005; Iliopoulos et al. 2009), graze year round in such areas. Although, some authors found that proximity of homesites to summer food sources increases pup survival, no direct links between homesite location and food abundance were recorded (Heard and Williams 1992; Heard et al. 1996; Frame et al. 2008). Breeding wolves may establish homesites even in areas far from abundant food resources and increase travel distance to feed offspring (Walton et al. 2001; Frame et al. 2008). In contrast, it seems that stability of food resources is more important and has been linked to den and rendezvous site selection (Ciucci and Mech 1992).

This is further supported by the lack of any significant influence of mean livestock density on rendezvous site selection. According to our findings, rendezvous sites were not related to prey abundance and were not located in proximity to each other, as shown by the low variation of the in-between rendezvous site distances, a pattern also encountered in northern Italy (Capitani et al. 2006). In fact, concentration of wolf rendezvous sites at areas with high livestock densities would result in respectively high inter-pack aggression and intra-specific mortality (Ciucci and Mech 1992). Appropriate spacing, to combine optimum distance from scattered food sources and reduced inter-pack aggression (Mech et al. 1998; Mech and Harper 2002), could be an important factor of rendezvous site spatial distribution apart for environmental and anthropogenic factors.

Regarding habitat types, wolves did not particularly select any specific forest habitat but generally avoided semi-forested areas and open habitats to establish rendezvous sites (w_i=0.52–0.57). Forest habitats offer greater safety from human disturbance and are usually selected for homesite establishment, even when open habitats dominate the landscape (Cortes 2001). In addition, evergreen scrublands were slightly preferred (w_i=1.38), although this preference was not statistically significant as dense or young forests appear to provide excellent hiding cover for wolves at homesites (Kaartinen et al. 2010).

At the home range scale, proximity to forest roads emerged as the most important factor (R=0.232), determining rendezvous site selection. As road proximity implies increased human disturbance, rendezvous sites were located away from forest roads at a high probability, corroborating results from studies in Italy (Ciucci et al. 1997; Capitani et al. 2006), Poland (Theuerkauf et al. 2003) and in a, heavily disturbed by logging, area in the USA (Person and Russell 2009). In effect, Karlsson et al. (2007) found that simple human presence in an area may trigger wolves to abandon it. Nonaka (2011) found that adult breeding wolves always moved away from dens up to 5,600 m after experimental disturbance at homesites and, in most cases, pups were translocated to a new den. Frame et al. (2007) found that pups were moved by adults to secondary dens in 50 % of all studied cases, following experimental disturbance. Nevertheless, this response was more related to pup age at the time of disturbance, as also found in India (Habib and Kumar 2007). Although wolves do not seem to tolerate human disturbance close to homesites (Frame et al. 2007; Argue et al. 2008; Habib and Kumar 2007; Nonaka, 2011), no effects between experimental human disturbance and survival of wolf pups were found (Frame et al. 2007; Argue et al. 2008; Person and Russell 2009). Wolves reused disturbed homesites at a similar frequency to undisturbed homesites, the years following disturbance (Frame et al. 2007; Argue et al. 2008; Person and Russell 2009). It is reasonable to assume that higher mobility of wolf pups in summer and early autumn makes them less vulnerable to human disturbance close to rendezvous sites as they can flee more easily from approaching humans compared to younger pups.

Nevertheless, in all aforementioned studies, experimental human disturbance did not include mortality of wolf pups or adult wolves. In contrast to experimental disturbance, in other cases when local residents are involved, presence of humans close to homesites may result in direct killing or removal of pups from dens (Jedrzejewska et al. 1996). Forty percent of wolves, aged less than 1 year in Greece, were killed inside homesites (Iliopoulos 1998), using the most commonly method, drive hunts. In fact, drive hunts are responsible for 42 % of overall human-caused mortality of adult wolves and 35 % of that of wolf pups (Iliopoulos 1998). The method consists of a hunting group walking inside wolf resting areas, with or without hunting dogs, and driving wolves in specific stalking points, similar to those for wild boar. This method is facilitated by forest roads which permit a quick census of wolf tracks around resting sites and an easier access of the hunting team. Road density was also highly correlated to increased harvest of wolves in southern Alaska (Person et al. 1996). In Bialowieza primeval forest, where a negative relation was similarly found between proximity to roads and rendezvous site selection (Theuerkauf et al. 2003), wolf pup human-caused mortality inside homesites has historically constituted an important factor of wolf mortality (Jedrzejewska et al. 1996). In our case, road avoidance by reproductive wolf packs, when selecting for rendezvous sites, may consist an adaptive strategy against hunting of breeding wolves and offspring in Greece, rather than a response to mere human presence and temporal disturbance.

The response to a particular disturbance seems to also depend on disturbance history, a critical concept in understanding the behavior of long-lived animals that learn through social transmission (Curatolo and Murphy 1986). Although this is the case for areas with increased anthropogenic impact and a long history of wolf persecution, in other areas where legal protection is implemented and human populations are low, no relations between distance from forest roads and rendezvous site selection has been detected (Unger et al. 2009). In such areas, some wolves seem to tolerate more human presence (Thiel et al. 1998).

Distance from villages was also related to anthropogenic disturbance, but with lower influence (R=0.151) on rendezvous site selection. Wolves selected sites that were farthest from villages, as also reported by Theuerkauf et al. (2003) and Capitani et al. (2006). However, in Greece, this factor was the least important because wolves frequent the vicinities of villages for food, such as garbage or dead livestock (Iliopoulos, unpublished data).

Proximity to water appeared to be the second most important factor (R=−0.209). Similar findings have been also reported by Unger et al. (2009) and Ausband et al. (2010). Proximity to water sources reduces the need for pups to travel longer distances and therefore expose themselves to fatal danger in order to drink water, which is essential for their survival, especially during summer and autumn dry months.

Another critical factor for rendezvous site selection at the home range scale was forest fragmentation (R=0.172). In our study sites, wolf packs selected for homogenous, less fragmented forested areas (see also Theuerkauf et al. 2003). In larger, more homogenous forests (higher TCAI index), potential predators (e.g., humans, livestock guarding dogs) need to travel longer distances inside vegetated areas to reach the centers of rendezvous sites and are subject to easier auditory detection by wolves as has been also experimentally demonstrated (Wam 2003; Karlsson et al. 2007).

Rendezvous sites appeared to be rather traditional, as a high rate of reuse was detected: the most notable cases involved reuse after 12 years and consecutive use for 5 years, while in total eight out of ten sites were reused for at least 2 years (Table 2). Wolf pack #5 used the same den and rendezvous site for at least five consecutive summers (2002–2007), whereas, according to local farmer testimonies, wolves bred there even earlier. After illegal killing of at least one breeder wolf in winter 2008, wolf reproduction ceased in that area. Forest network use at this homesite was restricted to public vehicles, with a system of metal bars set by the local hunting club to reduce hunting pressure. Moreover, livestock grazing was prohibited by forest service to protect black pine reforestations. Although we lack data on wolf reproduction prior to forest road closing in that area, consistent reuse of the den, and the associated rendezvous site, could be linked to low human presence. Another interesting reuse case of a rendezvous site that also encompassed a den in the same area was by wolf pack #1. Wolf reproduction was located for the first time during the onset of the study in spring and summer 1999. Although both radio-collared breeding wolves were illegally killed by wild boar hunters in fall 1999, reuse of the homesites was recorded after 12 years most probably by wolves unrelated to that first breeding pair.

Reuse rates of rendezvous sites in our study area are in partial contrast to results from Poland (Theuerkauf et al. 2003) or Finland (Kaartinen et al. 2010), where wolves used different homesites. Rendezvous site reuse has been associated with breeder persistence (Capitani et al. 2006) or with proximity to important or limited resources (Ballard and Dau 1983; Ciucci and Mech 1992). In our case, recorded reuse, apart from breeder persistence, may be also related to shortage of high suitability habitat for establishing new rendezvous sites. In fact, prediction maps at test areas showed that only 9.9 % could be suitable for rendezvous site core areas. This estimate may be even smaller, considering the variance not explained by the suitability model. As wolves appeared to select against human disturbance, and our study sites were located in areas with high human presence and very high forest road density, site reuse appeared as an ecologically safe option (see also Fernández et al. 2012).

Conclusions and management implications

The current study on wolf rendezvous site selection in northern and central Greece showed that avoidance of human presence and disturbance accounted more than factors related to habitat types or availability of prey. Wolf preference to livestock in our study area and the lack of any spatial association of rendezvous sites with prey availability are not contradictory, as free-ranging livestock also implies high human presence and disturbance. This strategy, adopted by wolves in Greece, may be a response to the long history of human persecution, still ongoing and widespread, and is consistent with countries with similar histories, such as Poland and Italy. This was more evident at the home range scale. On the other hand, at the landscape scale, wolves established rendezvous sites in a way to minimize intraspecific competition and maximize access to stable resource availability, a trend more commonly encountered among wolves (Ballard and Dau 1983; Fuller 1989a; Ciucci and Mech 1992).

Premium rendezvous site habitat appeared as a rather limited resource in our study area. This was expressed by the consecutive reuse of rendezvous sites by wolf packs and was highly related to high road density. Thus, control of forest road use could be an effective management measure to assist wolf reproduction in critical areas, such as sink areas with high human-caused mortality. A seasonal restriction on forest road use, implemented in parts of the study area to reduce hunting pressure, was also beneficial for wolves. Limited use of established road networks or careful planning of road network construction, along with maintenance of unfragmented forest patches, should always accompany any plans for establishment of protected areas in Greece, as by themselves do not seem to guarantee any particular positive effects on wolf demography. This perspective has been increasingly important for wildlife protection in national parks (Ament et al. 2008).

In the field, relatively accurate location of rendezvous sites was feasible through the howling survey method, which permitted cost-effective sampling of an increased number of different wolf packs and the creation of an RSF model suitable for large area assessment. As the RSF model robustness was adequate, it can be used with confidence to substantially concentrate wolf monitoring efforts on about 10 % of areas under consideration. A similar reduction (89 %) has been also reported by Ausband et al. (2010). Bearing this in mind, rendezvous site prediction maps can be variably useful during EIA studies. However, these maps are insufficient to predict and avoid permanent den site habitat modification or loss, caused by major infrastructure works.

In contrast, our rendezvous site prediction maps are valuable when permanent loss of rendezvous site habitat is in question. In Greece, they can be used for designing protected areas or for mapping livestock depredation risk. This is especially important since increased use of rendezvous sites partially coincides with the hunting season and human disturbance peaks or with attack peaks in autumn, respectively (Iliopoulos et al. 2009). Finally, when seasonal disturbance is considered, the assessment of rendezvous site maps should include individual and detailed disturbance time frames, as packs respond and are affected differently depending on the age of pups and the duration, season, and levels of disturbance (Habib and Kumar 2007; Argue et al. 2008; Person and Russell 2009).

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