Hystrix It. J. Mamm. (n.s.) 22(2) 2011: 269-279

SUMMER BED-SITE SELECTION BY ROE DEER IN A PREDATOR FREE AREA

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Received 2 February 2011; accepted 3 October 2011

ABSTRACT **-** For many animals, bed-site selection is influenced by anti-predator strategies, as they are forced to cope with high risk of predation. I examined summer bed-site selection by roe deer (*Capreolus capreolus bedfordi*) in an area - Baxianshan Nature Reserve, north China -, where predators were extirpated 22 years before, predicting that roe deer would select the bed-sites which allowed them to maximize fawn survival, independently from predation risk.

Among three available forest types, roe deer showed a strong preference for deciduous forests. Roe deer bedded at sites with higher elevation, denser shrub, higher herb biomass and cover and higher percentage of new shoots to the total twigs compared to negative sites. They selected bed-sites relatively far from trees, shrubs, and human features. Furthermore, roe deer avoided areas with tall shrubs and steep slopes. Principal component analysis (PCA) revealed that food availability, visibility, space, and human disturbance were the most important factors affecting bed-site selection by roe deer. Bed-site selection by roe deer was still the result of anti-predator strategies. This implies that two decades were a too short period to let deer lose the memory of predation pressure. This study suggests that the nonrandom bed-site selection of roe deer aimed to increase reproductive success by enhancing fawn survival.

Key words: *Capreolus capreolus bedfordi*, bedding behaviour, reproduction, anti-predator strategies

DOI: 10.4404/Hystrix-22.2-4571

INTRODUCTION

Habitat selection is a central theme in behavioral and evolutionary ecology, because the habitat may directly affect individual fitness (Doligez et al. 2002) and the evolutionary dynamics of populations (Forstmeier et al. 2001, Losos et al. 2003; Morris 2003; Leal and Fleishman 2004). Habitat selection results from the simultaneous consideration of many factors, including the need for forage, cover and predator avoidance (Ratikainen et al. 2007) and is the outcome of the trade-off between the costs and benefits connected with occupying each habitat (Lima and Dill 1990). Theoretical models predict that individuals should select habitats which allow them to increase their fitness by maximizing their survival and reproduction success (Orians and Wittenberger 1991).

Roe deer are a medium-sized, widespread species, ranging from temperate to sub-Arctic regions. The species has adapted to a wide variety of environments and habitats, showing a high level of ecological plasticity and success (Linnell et al. 1998; Lamberti et al. 2006). Studies on bed-site selection by roe deer have been carried out mainly in winter (i.e., Mysterud and Østbye 1995; Chen et al. 1999; Ratikainen et al. 2007), whilst a few studies were conducted in summer (Mysterud 1996; Linnell et al. 1999, 2004) or both seasons (Baltzinger 2003). Winter is considered to be a critical period for deer because of low temperatures and low availability and quality of forage. In this season, bed-site selection may be driven by the risk of hypothermia and food availability. In summer, which is the lactation period of roe deer, bed-site selection may be associated with the protection of fawns (Linnell et al. 1999).

Bed-site selection by roe deer has been found to be consistent with energy conservation and reducing the risk of predation (Mysterud and Østbye 1995; Linnell et al. 1999). In Baxianshan Nature Reserve (BNR), a poorly investigated forest habitat in northern China, the two potential predators of roe deer: the leopard (*Panthera pardus*) and wolf (*Canis lupus*) (Baskaya and Bilgili 2004; Bongi et al. 2008), were both extirpated in 1985 (BNR report, unpubl. data). Thus roe deer have been living in an area without predators for 22 years. While habitat use by roe deer has been well studied where there is a high risk of predation (Northern China, Chen et al. 1999), there is no information about habitat use in predator free areas, such as BNR. As this study was carried out during summer (i.e. the lactating season of roe deer), I predicted that roe deer would select the bed-sites which allowed them to maximize fawn survival, independently from predation risk.

STUDY AREA

This study was conducted at Baxianshan Nature Reserve (40°7′~40°13′ N, 117°7′~117°36′ E), north China. The study area covers 5360 ha with an altitude of 270-1056 m above sea level and has a continental monsoon climate. Annual mean temperature is 10.1°C (min-max: -21°C - 34.5°C), rainfall is about 968 mm, the main wet period lasting from May to August.

There are three forest types, coniferous, coniferous-deciduous and deciduous forests. The dominant overstorey trees are Mongolian oak (*Quercus mongolicus*), Mongolian linden (*Tilia mongolica*), black-bark pine (*Pinus tabulaeformis*), large-leaf Chinese ash (*Fraxinus rhynchophylla*) and Manchurian walnut (*Juglans mandshurica*). Dominant understorey shrubs include small flowered rhododendron (*Rhododendron micranthum*), point-leaved rhododendron (*R. mucronulatum*), shrub lespedeza (*Lespedeza bicolor*), hornbeams (*Carpinus turczaninowii*) and Manchurian lilac (*Syringa reticulata*). The dominant herbaceous layer includes reed grass (*Deyeuxia arundinacea*), fountain grass (*Pennisetum alopecuroides*) and bluegrass (*Poa* spp.).

In the study period, the density of roe deer was 3 to 5 individuals per 100 ha (Qin, unpubl. data). There was no other ungulate species in the study area. There were some villages and ranger stations in the study area, but most of them were far from survey transects (*Fig. 1*). Tourists occur from May to October and concentrate below 600 m a. s. l.

METHODS

1. Bed-sites survey

In July 2007 and 2008, surveys for bed-sites were conducted along ten transects, uni-

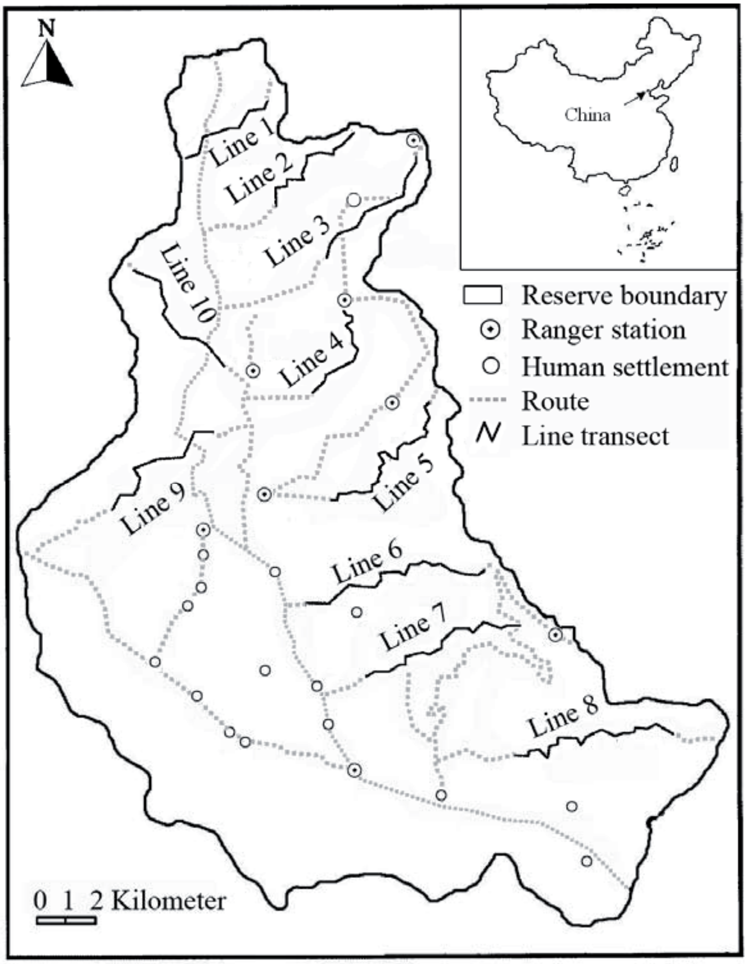

Figure 1 - Study area and location of survey routes.

uniformly distributed in the study area as to cover all forest types according to their relative availability (*Fig. 1*). The mean transect length was 11±2.6 km (min-max: 6.8-13.6 km). Two hundred 10×10 m^2 large plots were randomly established along these transects during the two years (126 in 2007 and 74 plots in 2008), recording the GPS location of the center of each plot. The distance between any two plots was more than 500 m. Most plots were visited only once. When the distance between two plots from each of the 2 years was less than 500 m, one of them was deleted to avoid clustering. At each plot, the presence of roe deer beds was recorded. Roe deer often scrape away loose material with their front hooves before bedding down, resulting in a clear lying-up mark (Mysterud and Østbye, 1995); however, only plots with both faeces and lying marks were identified as bed-sites. Nineteen habitat variables were recorded for both negative and positive for bed-sites plots (*Tab. 1*).

Table 1 - Habitat variables potentially driving bed-site selection by roe deer.

Variables	Abbreviation	Description
Elevation	Elevation (m)	Elevation above sea level.
Distance to water	DstWater (m)	Distance to the nearest point of water, determined from 1:10000 maps.
Distance to human	DstHuman (m)	Distance to the nearest point of roads or settlements, determined from 1:10000 maps.
Tree diameter at breast height	DiaTree (cm)	Measured by point-quarter sampling technique (Goldsmith and Harrison 1976).
Tree height	TreHeight (m)	Measured by point-quarter sampling technique.
Maximum tree canopy diameter	MaxTree (m)	Measured by point-quarter sampling technique.
Shrub height	ShuHeight (m)	Measured by point-quarter sampling technique.
Tree density	TreDensity	Total number of trees per plot.
Shrub density	ShuDensity	The total number of shrubs in the 1 m^2 large squares at the 4 corners of each plot.
Herb height	HerHeight (cm)	Mean herb height in the 1 m^2 large squares at the 4 corners of each plot.
Herb biomass	HerBiomass (g)	Mean herb biomass in the 1 m^2 large squares at the 4 corners of each plot.
Herb cover	HerCover (%)	Mean herb cover in the 1 m^2 large squares at the 4 corners of each plot.
Percentage of new shoots to the total twigs below 1 m	PerTwigs (%)	Mean percentage of new shoots to the total twigs below 1 m in the 1 m^2 large squares at the 4 corners of each plot.
Canopy closure of shrubs	CanShrubs (%)	Measure of the number of points under canopy closure at 0.5 m intervals at 15 m line intercept transects (Teng et al. 2004)
Concealment cover I	Concealment I	Mean visibility at 20 cm above ground (corresponding to a bedding deer) 5 m away along four cardinal directions. We used a 16-square 40×40 cm grid frame at the centre of the plot and counted the number of squares for which >50% of the area was visible.
Concealment cover II	Concealment II	Mean visibility at 120 cm above ground (corresponding to a standing deer); see Concealment I.
Slope	Slope (°)	Slope in the center of plot.
Tree distance	TreDistance (m)	Distance between each plot centre and the nearest tree.
Shrub distance	ShuDistance (m)	Distance between each plot centre and the nearest shrub.

2. Statistical treatment

Habitat selection among the different forest types was calculated according to Vanderploeg and Scavia's (1979) electivity index (E_i):

$$E_i = \frac{W_i - (1/n)}{W_i + (1/n)}$$

where n is the number of different forest types, and W_i, is defined by the equation:

$$W_i = \frac{G_i / X_i}{\sum (G_i / X_i)}$$

where G_i is the observed number of selected plots and X_i is the expected one. E_i can vary from –1 (avoidance) to +1 (selection).

In order to obtain normality and avoid heteroscedasticity, PerTwigs and CanShrubs were arcsin transformed, while Elevation, HerBiomass, DstWater and DstHuman were square root transformed. The chi-square goodness-of-fit test was employed to detect significant differences in bed-site location between forest types. The t-test was performed to compare plots positive for bed-sites *vs.* negative ones. Finally, a principal component analysis (PCA) was applied to identify which habitat variable accounted for the greatest variance. Values are reported as mean ±SE (standard error) and all tests were two-tailed.

RESULTS

A total of 64 plots were positive for bed-sites. The chi-square goodness-of-fit test indicated a significant difference between overall habitat availability and use ($x^2 = 11.28$, $df = 2$, $p < 0.01$). The electivity index showed a strong preference for deciduous forests (*Tab. 2*). In deciduous forest, shelter (Concealment I = 4±1.2) and food (Herbiomass = 620±60 g/m^2) conditions were better than those in the coniferous- (12±2.1 and 80±10 g/m^2, respectively) and coniferous-deciduous forests (8±2.0 and 395±50 g/m^2, respectively).

Roe deer tended to choose bed-sites in plots with higher elevation (72% of plots with elevation > 700 m), denser shrub (59% of plots with ShuDensity > 7 ind./4m^2), higher herb biomass (66% of plots with HerBiomass > 300 g), more herb cover (81% of plots with HerCover > 15%), higher percentage of new shoots to total twigs below 1 m (77% of plots with PerTwigs > 25%) and higher concealment cover I (67%of plots with Concealment I < 4) compared to negative plots. Additionally, most of bed-sites were located into plots farther away from trees (91% of plots with TreDistance >12m), shrub (65% of plots with ShuDistance > 2m), and human features (97% of plots with DstHuman >2000 m) than negative ones. In contrast, roe deer avoided bedding inside plots with taller shrub (69% of plots with ShuHeight < 0.8 m) and steeper slope (55% of plots with slope < 7°) (*Tab. 3*).

The first four principal components explained 66.21% of the total variance (*Tab. 4*). The first principal component (PC I) accounted for 21.75% of the variance, with positive loadings for HerCover (0.69) and PerTwigs (0.72), and negative ones for HerBiomass (-0.79). The second principal component (PC II) accounted for18.94% of the variance, with positive loadings for ShuDensity (0.86), ShuHeight (0.59), and Concealment I (0.87). The third principal component (PC III) accounted for 14.66% of the variance, with positive loadings for TreDistance (0.55) and slope (0.77), and negative ones for

Table 2 - Selection for forest type by roe deer.

Habitat type	G_i	X_i	W_i	E_i
Deciduous forest	56	82	0.73	0.38
Coniferous forest	1	16	0.07	-0.65
Coniferous-deciduous forests	7	38	0.20	-0.25

Table 3 - Habitat features of plots positive and negative for bed-sites (mean±SE; d.f. = 198).

Variables	Positive plots	Negative plots	*t*	*p*-value
Elevation (m)	722±26	594±14	5.93	0.000
DstWater (m)	1721±197	2024±121	-1.61	0.11
DstHuman (m)	2546±50	1441±80	9.55	0.000
DiaTree (cm)	26.96±11.79	29.69±10.07	-1.69	0.09
TreHeight (m)	14.67±4.09	15.00±3.82	1.13	0.26
MaxTree (m)	41.6±1.48	4.03±1.71	0.05	0.59
ShuHeight (m)	0.78±0.03	1.02±0.05	-2.99	0.000
TreDensity (ind./100m^2)	7.00±2.40	7.11±7.04	-0.12	0.900
ShuDensity (ind./4m^2)	7.28±3.00	4.85±3.78	4.62	0.000
HerHeight (cm)	37.39±9.50	35.96±13.85	0.75	0.460
HerBiomass (g)	614±91	181±24	6.00	0.000
HerCover (%)	26.87±1.26	9.40±2.10	5.08	0.000
PerTwigs (%)	33.50±1.71	17.95±2.50	6.20	0.000
CanShrubs (%)	16.67±0.91	19.24±0.79	-1.96	0.060
Concealment I	3.73±2.11	10.43±3.59	-14.71	0.000
Concealment II	11.53±2.68	11.24±2.81	0.71	0.480
Slope (°)	7.25±1.82	17.56±13.23	-6.20	0.000
TreDistance (m)	13.15±0.76	4.92±3.32	19.61	0.000
ShuDistance (m)	2.00±0.47	1.26±0.93	6.05	0.000

Table 4 - Principal component analysis (PCA) of habitat features on bed-sites.

Habitat features	PC I	PC II	PC III	PC VI
Elevation	0.03	0.00	0.11	0.84
TreDistance	0.42	-0.07	0.55	0.08
ShuDensity	0.04	0.86	0.03	-0.06
ShuHeight	-0.47	0.59	0.08	-0.40
ShuDistance	0.38	0.04	-0.72	0.18
HerBiomass	-0.79	-0.16	-0.02	0.04
HerCover	0.69	-0.39	-0.19	-0.20
PerTwigs	0.72	0.14	-0.27	0.07
Slope	-0.15	0.15	0.77	0.09
Concealment I	0.19	0.87	0.00	0.04
DstHuman	-0.41	-0.12	-0.27	0.48
Eigenvalue	2.62	2.110	1.42	1.14
Explained variance (%)	21.75	18.94	14.66	10.85
Total explained variance (%)	21.75	40.69	55.36	66.21

ShuDistance (-0.72). The fourth principal component (PC IV) accounted for 10.85% of the variance, with positive loadings for Elevation (0.84) and DstHuman (0.48), respectively.

DISCUSSION

An earlier study from northeastern China showed that roe deer preferentially selected bed-sites in coniferous forest, which offered higher canopy closure with respect to the other available habitats (Chen et al. 1999). The selection for sites with a high canopy closure may be interpreted as an anti-predator strategy (Smith et al. 1986). In Arizona, preference of mule deer for bed-sites in coniferous forest has also been related to shelter conditions (Germaine et al. 2004). In the study area, roe deer avoided bedding in coniferous forest, suggesting that their bed-site selection may not be driven by anti-predator strategies. On the contrary, PCA showed that visibility was a major habitat feature, which has been shown to be related to the avoidance of predators (Bongi et al. 2008). Although these results are apparently discordant, I suggest that bed-site selection by roe deer in BNR may still be an anti-predator strategy for the following reasons.

Firstly, both the study of Chen et al. (1999) and Germaine et al. (2004) were both carried out in seasons –winter and summer respectively-, when the highest concealment cover was actually found in coniferous forests. In BNR, shelter conditions were better in the deciduous forest than the coniferous one. Secondly, Berger et al. (2001) found that ungulates which had previously been unfamiliar with dangerous predators for as few as 50 to 130 years, learned appropriate anti-predator tactics within only one generation. This suggests that 22 years may not be enough for roe deer to lose the memory of predation pressure. Thirdly, some anti-predator behaviours may be inheritable (Cousyn et al. 2001). Therefore, I argue that, contrary to my prediction, in BNR roe deer bedding in deciduous forest may be the result of anti-predator strategies.

The principal component eigenvalues reflect the relative importance of variables (= habitat features) (Kostrzewa 1996). In this study, the four principal components can be designated as food availability, visibility, space and human disturbance, respectively. These habitat features were the most important factors affecting bed-site selection by roe deer.

Food availability is regarded as critical for the nutrition of both fawns and female roe deer in summer (Pettorelli et al. 2005). Being concentrate selectors, roe deer depend on high quality food (Hofmann 1989) and often bed next to high quality feeding sites (Mysterud et al. 1999, Vospernik et al. 2007). Ward et al. (2008) reported that roe deer did not eat conifers. Accordingly, in BNR only one bed-site was found in the conifers during the study period. In this study area, deciduous forest offered the highest availability of palatable understory vegetation for roe deer and the highest herb biomass. Roe deer were recorded feeding on more than 50 species of plants, *ca.* 90% of which were found in deciduous forest (Qin, unpubl. data). The results suggest that, by bedding in deciduous forest, roe deer might aim to increase their reproductive success through ensuring optimal feeding to fawns.

The variables shrub density, shrub height and concealment cover I can be related to decreasing visibility by predators. In contrast, concealment cover II did not differ between plots positive and negative for bed-sites, suggesting that roe deer select bed-sites which offer the best protection for fawns, which often hide in the shrubs while their mother is looking for food (Bongi et al. 2008).

In general, the selection for steeper slopes is associated to the need for safe shelter (Gavashelishvili 2004; Adrados et al. 2008). In contrast, in BNR, roe deer preferred flatter slopes as bed-sites. Similar results were obtained on mule deer by Smith et al. (1986), who suggested that the proximal cause of this preference is the need for space during lactation. Accordingly, in BNR most bed-sites were far away from trees and shrubs, which may provide roe deer with more space. During lactation, roe deer fawns lie concealed for long periods (e.g. Bongi et al. 2008) and may move around only after the return of their mother. Bedding in flat and open places may therefore provide a comfort space for fawn movements.

Human presence may be stressful to deer (Sauerwein et al. 2004) and distance from human settlements has been shown to be an important factor determining habitat selection by roe deer (Ratikainen et al. 2007). As reported for East Caucasian tur (*Capra cylindri-*

cornis) in Georgia (Gavashe-lishvili 2004), roe deer might avoid lower elevations also because of human disturbance.

The bed-sites of roe deer do not allow the recognition of the sex of the individual who used them in the present study. This limit could partly impair the interpretation of the results as bed site selection aimed to increase fawn survival. Although line transect surveys are widely used in animal population ecology when budgets are limited (Olson et al. 2005; Focardi et al. 2005) and pellet counts have been shown to yield as sound information as radio-telemetry about habitat use by deer (Guillet et al. 1995), only the latter method may allow one to distinguish the behaviour of the two sexes. However, in BNR roe deer are most commonly sighted in groups of 3 to 5 individuals, of which 2 to 4 individuals are females (Qin, unpubl. data). During the study period, roe deer were observed in six occasions, of which four occasions included fawns. These sightings may indicate that bed-sites were most probably used by females with fawns. In any case, further research is needed on bed site selection by roe deer through radio-tracking, in order to clarify the patterns of habitat use by different sexes and age classes.

ACKNOWLEDGEMENTS

This work was supported by the Fund of Wildlife Investigation in Baxianshan Nature Reserve. I would like to thank Tiejian Zhao, Jinbao Zhu, Guoming Sun and Xiaomei Feng for their valuable help in the field, and, particularly, Xiubai Ren for permission to conduct the fieldwork. I am very grateful to two anonymous reviewers who provided helpful advice regarding the early draft of this paper. Special thanks to Cassandra Smith, University of Wollongong (Australia), who kindly revised my English.

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