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BEHAVIORAL ECOLOGY - ORIGINAL PAPER

Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales

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Abstract We examined the relationship between survival of roe deer (*Capreolus capreolus*) fawns at Trois Fontaines, Champagne-Ardennes, France, and factors related to bed-site selection (predator avoidance and thermoregulation) and maternal food resources (forage availability in the maternal home range). Previous studies have demonstrated that at small scales, the young of large herbivores select bed sites independently from their mothers, although this selection takes place within the limits of their mother's home range. Fawn survival was influenced largely by the availability of good bed sites within the maternal home range, not by the fawn's selection of bed sites; however, selection for thermal cover when selecting bed sites positively influenced survival of young fawns. Typical features of a good home range included close proximity to habitat edges, which is related to forage accessibility for roe deer. The availability of bed sites changed as fawns aged, probably due to an increased mobility of the fawn or a different use of the home range by the mother; sites offering high concealment and thermal protection became less available in favor of areas with higher forage accessibility. Despite the minor influence of bed-site selection on survival, roe deer fawns strongly selected their bed sites according to several environmental factors linked to predator avoidance and thermoregulation. Fawns selected for sites providing concealment, light penetration, and avoided signs of wild boar (*Sus scrofa*) activity. Avoidance of sites with high light penetration by young fawns positively affected their survival, confirming a negative effect on thermoregulation due to reduced thermal cover. Selection for light penetration by older fawns was less clear. We discuss these results in the context of cross-generational effects in habitat selection across multiple scales, and the potential influence of the 'ghost of predation past'.

Keywords *Capreolus capreolus* · Habitat selection · Predation · Roe deer · Predation

Introduction

In most populations of large herbivores, juvenile survival is relatively low and variable compared to adult survival (Gaillard et al. 1998b; Eberhardt 2002), so that variation in juvenile survival is potentially an important contribution to changes in population dynamics (Gaillard et al. 2000; Coulson et al. 2005). For instance, annual variation in

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survival of neonates over their first summer was found to be a major factor in the population dynamics of elk (*Cervus elaphus*) in Jackson, Wyoming (Lubow and Smith 2004), of mule deer (*Odocoileus hemionus*) in west central Colorado (Pojar and Bowden 2004), of white-tailed deer (*Odocoileus virginianus*) in western Oregon (Ricca et al. 2002), or of moose (*Alces alces*) in eastern interior Alaska (Bertram and Vivion 2002). Understanding the basis of variation in juvenile survival both among species but also within populations is thus important to our understanding of population dynamics of large herbivores.

In large herbivores, juveniles can be ranked along a continuum according to the tactic they adopt to minimize the risk of predation, from those that follow their mothers continuously (‘followers’) to those that rely on hiding while their mothers forage (‘hiders’) (Walther 1965; Ralls et al. 1986) during the early postnatal period (from some days to several weeks; Lent 1974). Followers are typically species where the fawn receives continuous protection from its mother as it consistently follows its mother from birth to weaning [e.g., wildebeest (*Connochaetes taurinus*), Estes and Estes 1979]; whereas animals that adopt a hiding tactic [e.g., pronghorn (*Antilocapra americana*), white-tailed deer, roe deer (*Capreolus capreolus*)], rely on their bed site both to hide from predators and to protect themselves from adverse influences of microclimate (e.g., Alldredge et al. 1991; Canon and Bryant 1997; Linnell et al. 1999; Tull et al. 2001).

Where hiding tactics are involved, selection of a bed site is not different from other types of habitat selection, which is, as pointed out by Johnson (1980), a hierarchical process. The selection of a bed site by a fawn takes place within the limits of the maternal home range. The general location of the bed site is thus largely determined by the mother; however, the actual bed site is chosen by fawns [Bubenik 1965; Epsmark 1969 (at the scale of 1 ha); Johnson 1982; White et al. 1972].

The adaptive significance of the hider strategy is considered to be predator avoidance [reviewed by Caro (2005)]. For example, hiding by Thomson’s gazelle (*Gazella thomsoni*) fawns decreases the probability of them being found by cheetahs (*Acinonyx jubatus*) (FitzGibbon 1990). Three fawn characteristics contribute to the effectiveness of the hider strategy. First, there is a very strong relationship between cryptic coat coloration and the hiding strategy; all species with spotted young are hiders (Stoner et al. 2003). Second, movement facilitates detection by predators, and relatively short and few active periods are expected from hiders, as was found for white-tailed deer (Jackson et al. 1972). Finally, efficient hiding depends on concealment provided by the hiding place; therefore, a careful selection of the bed site is expected. In many hider species the bed site provides more cover and concealment than would be expected from random selection [e.g., roe deer (Linnell et al. 1999), pronghorn (Canon and Bryant 1997), and white-tailed deer (Huegel et al. 1986)].

Early-life survival is very sensitive to climatic conditions (Gilbert and Raedeke 2004; Jones et al. 2005); hypothermia has been shown to be one of the most important causes of fawn mortality in the absence of predators (Andersen and Linnell 1998; Olson et al. 2005). In particular, the period shortly after birth is critical due to limited energy reserves and the small body size of fawns [reviewed for lambs (*Ovis aries*) by Nowak and Poindron (2006)]. The protection provided by bed sites against climatologic influences therefore is expected to be important. White-tailed deer fawns select for sites offering thermal comfort, while offering maximum hiding opportunities (Huegel et al. 1986). Linnell et al. (1999) showed that there is usually a large amount of low ground cover at the bed sites of roe deer fawns, as well as a high amount of canopy cover. Ground cover provides insulation from heat loss due to conductance towards the bare soil and canopy cover is known to provide thermal cover for large herbivores (Cook et al. 2005).

In addition to conditions and features of bed sites, the availability of forage at the level of the home range is expected to play a major role in the survival of fawns. For income breeders such as roe deer (Andersen et al. 2000), incoming energy, not fat reserves like in the case of capital breeders [e.g., red deer or bighorn sheep (*Ovis canadensis*) among large herbivores], is used by mothers to raise their young (Jonsson 1997). Thus, food availability in the maternal home range is important to sustain the high energetic requirements for lactation.

While evidence of bed-site selection and the identification of the environmental factors driving that selection have been reported in several studies, these factors have largely been related to juvenile survival only by anecdote or circumstantially. Moreover, the influence of hierarchical scales of bed sites selected by fawns within the seasonal home range selected by the mother have not been properly addressed. Here we examined direct relationships between survival of roe deer fawns at Trois Fontaines, Champagne-Ardennes, France (e.g., Gaillard et al. 1993; McLoughlin et al. 2007), and factors related to bed-site selection (predator avoidance and thermoregulation) and maternal food resources (forage availability in the maternal home range). High variation in juvenile survival both among years (Gaillard et al. 1997) and across space in a given year (Pettorelli et al. 2005) make the species ideal for investigating links between juvenile survival and bed-site selection by fawns, and availability of suitable bed sites and forage within the maternal home range. According to the anti-predatory origin of the hider strategy, we expected roe deer fawns to select bed sites that provided concealment from predators. To protect themselves against hypothermia fawns should select for ground cover at bed sites that provide insulation from the bare soil, and sites with closed canopy cover to provide overhead thermal cover. The availability of forage resources should not play a role in the small-scale selection of the bed site; however, as discussed above, at the scale of the maternal home range we expect it to affect fawn survival. Thus, accessibility of edges in the maternal home range—which have been shown to have high forage and are important to roe deer (Said and Servanty 2005; McLoughlin et al. 2007)—should increase the probability of fawn survival. We discuss our results in the context of resource selection across multiple scales, and the potential role of the 'ghost of predation past' (Peckarsky and Penton 1988; Byers 1997).

Materials and methods

Study site

Our study was performed at the Territoire d'Etude et d'Expérimentation at Trois Fontaines, a 1,360-ha enclosed forest reserve, divided into 172 forest census plots (7.3 ± 1.7 ha, $\bar{x} \pm 1$ SD) and situated in north-east France (Champagne-Ardennes, 48°43′N, 2°61′E). Trois Fontaines has a continental climate characterized by cool winters (mean daily temperature in January is 2°C) and hot, but not dry summers (mean daily temperature in July is 19°C and total rainfall July–August is 130 mm). The forest overstory is dominated by oak (*Quercus* spp.) and beech (*Fagus sylvatica*), and the coppice by hornbeam (*Carpinus betulus*).

At Trois Fontaines, predation is not expected to be of large importance to fawn survival. Due to the minimal odor presented by fawns (Jackson et al. 1972), predators mostly rely on vision when hunting fawns. The visual hunting strategy used by red fox (*Vulpes vulpes*)—shown to be the major predator of roe deer fawns in Sweden (Jarnemo 2004; Jarnemo and Liberg 2005)—is not likely to be efficient in the dense beech and oak forests of our study site. In addition, the density of foxes at Trois Fontaines is relatively low (D. Delorme, personal observation). Other predators of fawns at Trois Fontaines, which also appear in low abundances, may include wild cats (*Felis silvestris*) (Delorme and Léger 1990).

In a previous study at our site (Gaillard and Delorme 1989), we found that fawns avoided signs of wild boar activity. The impact of wild boar for our current study might have changed due to a marked decline in wild boar population density after 1991; this makes a direct comparison of our current study with the one from 1989 difficult. In 1991, the study site at Trois Fontaines became a Territoire d'Etude et d'Expérimentation, thereafter the hunting of boar increased drastically. This resulted in a population decline of almost half; a significant number of wild boar are, however, still present in the reserve.

Data collection

In 1992 and 1994–1997, we located 147 roe deer fawns (17, 23, 28, 41 and 38 individuals by year; 1:1 sex ratio) in the study area during the season of births (May–June). We located fawns by systematically searching areas where parturient does were observed; the fawns included in this study were distributed rather evenly over the whole study site. The age of fawns was estimated by wear on hoof cartilage, the appearance of the umbilical cord, or behavior of the fawn (Jullien et al. 1992). Ages of the located sample of fawns ranged from 1 to 12 days [mean (SD): 4.8 (3.2) days].

For each fawn, we described microhabitat within the square meter of the bed site, which we paired with one quadrat of the same size placed 50 m north of the bed site. For both sites, we measured: (1) visibility of the fawn by the observer due to the amount of understory surrounding the fawn (a categorical variable coded as visible, half-visible, and concealed); (2) extent of insulation from the soil by ground cover as offered by the presence of dead leaves and/or herbaceous plants, which we recorded as a binary variable (i.e., bare ground or with cover); (3) canopy cover was measured by the light penetrating through the canopy (coded as a categorical variable: light, half-shaded, and shaded); and (4) distance (m) from the site towards the nearest edge (e.g., habitat transition or road). In addition, signs of wild boar activity (i.e., tracks, indices of foraging activity) within a radius of 10 m around the bed site were examined and recorded as a binary variable (absence or presence of such signs). As mentioned above, the latter has previously been shown to negatively affect fawn bed-site selection (Gaillard and Delorme 1989). The exposing of soil by wild boar also has been suggested to result in decreased ground cover for roe deer fawns [although no evidence for that was found from our data ($r = -0.08$, $t = -0.99$, $df = 145$, $P = 0.33$)], which might affect the ability of fawns to thermoregulate. As the ability of fawns to thermoregulate is likely dependent on weather conditions, we included three meteorological variables [daily total precipitation (in mm), and minimum and maximum daily temperatures (in °C)] for each fawn at their date of capture (data available from the Météo-France weather station of Saint-Dizier located at less than 5 km from the study site).

During winter, intensive capture sessions were organized (see Gaillard et al. 1993 for a description of capture procedures). These capture sessions allowed us to determine whether a fawn survived in the study area or not [mean survival rate for the different years was, respectively: 0.59, 0.57, 0.61, 0.37, and 0.45 (Gaillard et al. 1998a)]. The large proportion of animals captured each year during these sessions, together with the high survival probability of adult animals, provided us with reliable fates for monitored fawns early in life [see Gaillard et al. (1998a) and Gaillard et al. (1998a, 2005) for further justification].

Data analysis

To assess habitat characteristics that influenced bed-site selection of roe deer fawns, we considered bed-site selection as a discrete choice between the observed bed site and the paired empty site. The paired control site might be used as a future bed site, thus leading to contamination of the sample (Keating and Cherry 2004), but the large number of available sites for bed sites makes the future use of exactly the paired control highly unlikely. We can therefore be confident that the occurrence of contamination will be low, leading to a negligible bias of our results (Johnson et al. 2006). The analysis suggested by Manly et al. (2002, p. 152) for these discrete-choice problems is a logistic regression using the difference scores for the habitat variables between the selected and the paired site with a zero intercept. We thus modeled selection based on the difference scores. In all analyses, age was standardized to allow convergence of the model-fitting algorithm (consequently all ages lower than the mean of 4.8 days were negative).

To analyze the impact of bed-site selection on fawn survival, we compared the habitat selection of surviving versus dying fawns [see comparable approach for caribou (*Rangifer tarandus*) by McLoughlin et al. (2005)]. We again used the difference between the observed bed site value for a given variable and that of the paired site as a measure of selectivity. We used logistic regression of these difference scores to predict survival of fawns.

Bed-site selection is the difference between the used bed site and the available paired site, thus changes in available sites might lead to changes in selection. Age effects in the previous analyses on bed-site selection might be caused by changed availability. We investigated changes of available sites as fawns aged using linear regression and logistic regression (for the binary variables, see Table 1).

For the effect of availability of the different habitat variables within the maternal home range on survival, we used the paired empty site as a random sample from the mother's home range. To decrease the impact of sampling errors, we pooled all samples for each forest census plot; we thus used the mean sample value for each forest plot. Adult home ranges in Trois Fontaines are about 25 ha (Said and Servanty 2005), thus this reduction in spatial resolution will not lead to the loss of important information. Using logistic regression, we investigated the importance of various habitat measures at the home range level on the survival of fawns.

We used information-theoretic criteria for model selection: Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We selected models using a backward model fitting procedure (Searle 1971) and so checked for local minima by adding each omitted variable again to the final model. All models with a likelihood higher then 0.25 of being the best model from the set of models fitted were considered. The importance of each variable was then assessed using the cumulative Akaike weights of the models with this variable (i.e., the relative variable importance); this value represents the probability that the variable would be present in the Kullback–Leibler best model (Burnham and Anderson 2002). In all models for fawn survival we included a cohort effect as a correction for the marked among-year variation in fawn survival shown in that roe deer population (e.g., Gaillard et al. 1997). Meteorological conditions were included in interaction with variables related to thermoregulation in the final models to investigate whether they would lead to improved fit.

Table 1 Different measures used to describe bed sites and paired random sites

Measure	Levels	Biological significance	Mean (SD) of the bed site	Mean (SD) of the paired site
Ground cover of fallen leaves or herbaceous plants	Binary: bare ground versus cover (1–0)	Thermoregulation (insulation from the ground)	0.87 (0.33)	0.83 (0.38)
Concealment	Categorical: not, half and concealed (0–0.5–1)	Predator avoidance and thermoregulation	0.42 (0.28)	0.20 (0.33)
Light penetration through the canopy and understory	Categorical: shadow, half and light (0–0.5–1)	Thermoregulation (thermal cover)	0.66 (0.47)	0.64 (0.48)
Distance towards edge	Continuous: distance in meters	Proximity of forage	51 (38)	56 (50)
Wild boar activity	Binary: presence or absence (0–1)	Thermoregulation (and predation)	0.20 (0.40)	0.35 (0.48)

Table 2 Number of parameters (K), Akaike's information criterion corrected for small sample sizes (AIC_c), ΔAIC_c, likelihood (L) and Akaike's weight (w) for models from the habitat selection analysis

Models[a]	K	AIC_c	ΔAIC_c	L	w
0 + light × age + concealment × age + wild boar	6	135.25	0.00	1.00	0.72
0 + light × age + concealment × age + wild boar × age	7	137.09	1.85	0.40	0.28

[a] Models are in the order of descending likelihood

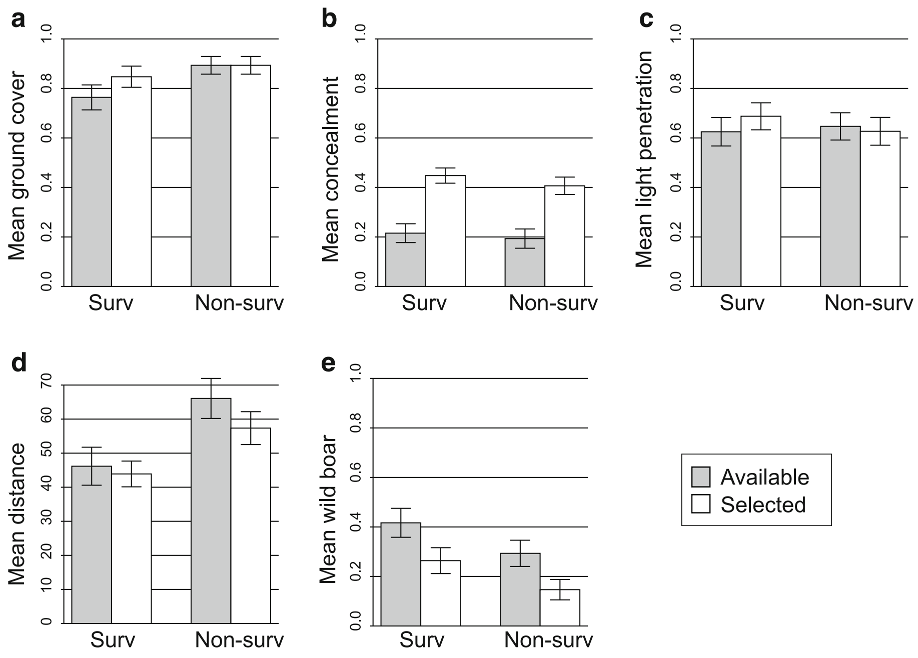

Fig. 1 Mean values of five environmental variables of used and available bed sites of surviving (*Surv*) and dying fawns (*Non-surv*). *Grey bars* show the paired available sites, *white bars* the observed bed sites. **a** Ground cover in quadrants, **b** concealment of fawn, **c** light penetration, **d** distance towards edge, **e** signs of wild boar activity

We used R 2.5.0 (R Development Core Team 2005) for all statistical analyses.

Results

Preliminary considerations

Co-linearity was not a problem in our data: the highest correlation coefficient (between light penetration and concealment) only reached −0.37, all others being smaller than $|r| = 0.15$. Consistent with previous analyses on the same population (Gaillard et al. 1997; Gaillard et al. 1998a), we did not find any evidence for between-sex differences in fawn survival (0.52 and 0.47 for males and females, respectively, $t = 0.65$, $df = 143$, $P = 0.51$); hence, we pooled data for both sexes in all analyses.

Fawn bed-site selection within the maternal home range

From the best-fitting models (Table 2), three habitat variables were involved in bed-site selection (Table 5). Fawns selected for sites with higher light penetration [Figs. 1c, 2; 1.98 ± 0.54 (slope ± SE), $z = 3.68$, $df = 141$, $P < 0.0001$] and higher concealment [Figs. 1b, 3; 4.83 ± 0.91 (slope ± SE), $z = 5.31$, $df = 141$, $P < 0.0001$] as compared to random locations, and avoided locations where there were signs of wild boar activity [Fig. 1e; -1.43 ± 0.47 (slope ± SE), $z = -3.00$, $df = 141$, $P < 0.0001$]. The intensity of selection for sites with higher light penetration increased with fawn age [change in slope with increasing age, 1.23 ± 0.50 (slope ± SE), $z = 2.46$, $df = 141$, $P < 0.015$]; as did effects of selection for areas with high concealment [change in slope with age, 3.50 ± 0.96 (slope ± SE), $z = 3.65$, $df = 141$, $P < 0.0001$].

No improvement of fit was gained by including effects of light penetration and any meteorological variables (ΔAIC_cs for precipitation, minimum and maximum temperature were 1.75, 1.53, and 4.09, respectively). However, light penetration tended to be preferred when the daily maximum temperature was higher [change in slope with temperature, 0.72 ± 0.47 (slope ± SE), $z = 1.52$, $df = 139$, $P = 0.13$].

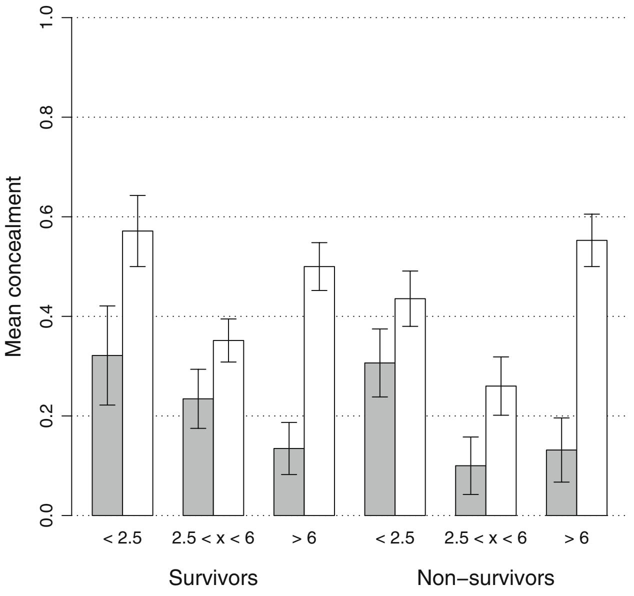

Fig. 2 Influence of age on the relationship between fawn survival and light penetration. *Grey bars* show the paired sites, *white bars* observed bed sites. *x-axes* indicate age of fawns. *Survivors* Surviving fawns, *Non-survivors* fawns that died

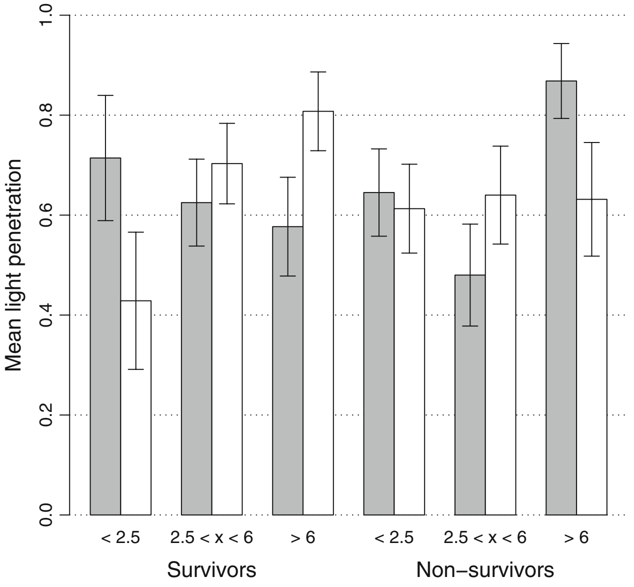

Fig. 3 Effect of age on the relationship between fawn survival and concealment. *Grey bars* show the paired sites, *white bars* observed bed sites. *x-axes* indicate age of fawns. For abbreviations, see Fig. 2

Influence of fawn bed-site selection within the maternal home range on their survival

For the effect of bed-site selection on survival all models included a cohort effect as a correction for the marked among-year variation in fawn survival reported previously (Gaillard et al. 1997). The positive effect of fawn age on survival [0.36 ± 0.21 (slope ± SE), $z = 1.77$, $df = 139$, $P = 0.07$] was included in top-ranking models (Table 3). Light penetration was another variable that received strong support (Tables 3, 5). Avoidance of sites with light penetration positively affected survival in younger fawns, whereas selection for such sites increased survival of older fawns [Figs. 1c, 2; change in slope with increasing age, 1.03 ± 0.35 (slope ± SE), $z = 2.93$, $df = 139$, $P = 0.003$].

Age effects on the available sites within the maternal home range

Two variables showed a significant change in available sites (i.e., paired site) within the home range as fawns aged: older fawns have less ground cover [−0.42 ± 0.22 (slope ± SE), $df = 145$, $P = 0.049$], and less concealment [−0.060 ± 0.027 (slope ± SE), $df = 145$, $P = 0.028$] available than younger fawns. The available distance towards edges shows a strong tendency to decrease with age [−7.7 ± 4.1 (slope ± SE), $df = 145$, $P = 0.06$). We did not report any age-related changes of signs of wild boar activity [−0.044 ± 0.174 (slope ± SE), $df = 145$, $P = 0.8$] or available light penetration [0.019 ± 0.040 (slope ± SE), $df = 145$, $P = 0.63$]. In the previous analysis we did find, however, an important effect of light penetration on survival; therefore, we analyzed both survival categories separately. The bed sites of surviving fawns did not show a detectable change of available light penetration with age [−0.063 ± 0.058 (slope ± SE), $df = 70$, $P = 0.27$]; however, those of the non-surviving fawns did: sites of older non-surviving fawns had more available light penetration [0.111 ± 0.057 (slope ± SE), $df = 73$, $P = 0.05$].

Impact of the available sites within the maternal home range on fawn survival

Besides the cohort effect (included to correct for among-year variation in fawn survival) and the increased survival when fawns aged [1.06 ± 0.45 (slope ± SE), $z = 2.37$, $df = 138$, $P = 0.02$], the availabilities of two environmental variables in the maternal home range received strong support for their impact on fawn survival (Tables 4, 5). The influence of the distance towards edges on fawn survival was strongly supported (Tables 4, 5): fawn survival increased with the decreasing distance towards edges in their home range [Fig. 1d; −0.011 ± 0.005 (slope ± SE), $z = -2.10$, $df = 138$, $P = 0.04$]. Surprisingly, the influence of light penetration on fawn survival also received strong support (Tables 4, 5): availability of light penetration had an increasingly negative effect on fawn survival as they aged [Figs. 1c, 2; change of slope with increasing age, −1.17 ± 0.57 (slope ± SE), $z = -2.05$, $df = 138$, $P = 0.04$].

Table 3 *K*, AIC$_c$, ΔAIC$_c$, *L* and *w* for the models of the effect of habitat selection on survival analysis. For abbreviations, see Table 2

Models[a]	*K*	AIC$_c$	ΔAIC$_c$	*L*	*w*
Cohort + light × age	8	200.77	0.00	1.00	0.29
Cohort + light × age + distance	9	201.71	0.95	0.62	0.18
Cohort + light × age + distance × age	10	201.92	1.15	0.56	0.16
Cohort + light × age + ground	9	202.58	1.82	0.40	0.12
Cohort + light × age + wild boar	9	202.86	2.10	0.35	0.10
Cohort + light × age + concealment	9	202.99	2.22	0.33	0.10
Cohort + light × age + ground × age	10	203.47	2.70	0.26	0.08

[a] Models are in the order of descending likelihood

Table 4 *K*, AIC$_c$, ΔAIC$_c$, *L* and *w* for the models of the effect of the home range on survival analysis. For abbreviations, see Table 2

Models[a]	*K*	AIC$_c$	ΔAIC$_c$	*L*	*w*
Cohort + light × age + dist	9	203.84	0.00	1.00	0.31
Cohort + age + dist	7	204.83	0.99	0.61	0.19
Cohort + light × age + ground × age + dist	11	205.67	1.83	0.40	0.13
Cohort + light × age + ground + dist	10	205.99	2.15	0.34	0.11
Cohort + light × age + ground + dist + wild boar × age	12	206.31	2.47	0.29	0.09
Cohort + light × age	8	206.39	2.55	0.28	0.09
Cohort + light + age + dist	8	206.41	2.56	0.28	0.09

[a] Models are in the order of descending likelihood

Table 5 Cumulative *w* for each variable from the three analyses

Variables	Bed-site selection[a]	Survival selection[b]	Survival available[c]
Light	1	1	0.81
Concealment	1	0.1	0
Ground	0	0.19	0.32
Dist	0	0.35	0.91
Wild boar	1	0.1	0.09
Light × age	1	1	0.72
Concealment × age	1	0	0
Ground × age	0	0.08	0.13
Dist × age	0	0.16	0
Wild boar × age	0.28	0	0.09

[a] *w* for bed-site selection analysis

[b] *w* from the effect of selection on survival analysis

[c] *w* from the effect of the home range on survival analysis

Discussion

As expected, we found that fawns were highly selective when choosing their bed site. Supporting the anti-predator function of the hider strategy (Walther 1965; Ralls et al. 1986), we found a strong selection for cover variables important to concealment at bed sites. The absence of an effect of concealment on fawn survival confirms our supposition that predation was of no importance in our study site. The importance of concealment in the selection of bed sites, while it does not affect fawn survival at our study site, supports a 'ghost of predation past' interpretation (Peckarsky and Penton 1988; Byers 1997) in a current environment with predators being mostly absent. Increased selection with age for concealed bed sites seems to be largely due to a decrease in available habitats offering opportunities for concealment with age (Fig. 3).

Contrary to the study of Linnell et al. (1999), we found fawns selecting sites with greater light penetration (i.e., less canopy cover) for their bed site. This seems to be especially true for older fawns (Fig. 2); for younger fawns, however, there is an avoidance of light penetration. This strong age interaction supports our thermoregulation interpretation, where light penetration is inversely related to the thermal cover provided by canopy. The absence of interactive effects of bed site characteristics and meteorological conditions is therefore surprising. However, the tendency we found here was confirmed in supplementary analyses (not reported here): canopy cover was preferred on days with a low maximum temperature, whereas light penetration was sought for on warmer days. We can speculate about the animals searching for exposure to sun on sunny days, whereas on cloudy days fawns would prefer the thermal cover provided by canopy. Further analyses would be required to test firmly such hypotheses.

Confirming a previous study at our site (Gaillard and Delorme 1989), we found that fawns avoided signs of wild boar activity. Gaillard and Delorme (1989) suggested that the clearing of ground cover by foraging wild boar might lead to an indirect avoidance of wild boar through the avoidance of bare soil. However, we did not find evidence supporting this presumed relationship between wild boar and bare soil at the available sites. This could be explained by a marked difference in wild boar population density between both study periods (after 1991 wild boar population declined by almost half, see "Materials and methods"). Wild boar avoidance was no longer expected after accounting for the presence of ground cover. Despite the lower population density of wild boar and the fact that we controlled for ground cover, we still found avoidance of wild boar by fawns in the selection of their bed site. The absence of an effect of wild boar activity on survival makes wild boar predation an unlikely explanation. We therefore suggest that the effect of wild boar on bed-site selection might be a mere consequence of the disturbance associated with their activity.

Survival probabilities of roe deer fawns increased markedly with age, which underlines the critical nature of early fawn survival for roe deer. Available bed sites within the maternal home range (i.e., large spatial scale) and the selection of the bed site constrained within this home range [i.e., fine scale, smaller than 1 ha (Epsmark 1969)] by fawns appeared to affect the survival of fawn in a different way (Table 5). As expected, the distance to edges only influenced survival at the home range scale and not at the bed-site-selection scale. For income breeders like roe deer (Andersen et al. 2000), the availability of good-quality forage is crucial to provide the necessary energy to sustain the increased demand due to lactation. Access to edges with their associated forage availability (Said and Servanty 2005) was therefore expected to increase survival probabilities of the fawn. Recently, access to edges was also linked to lifetime reproductive success of female roe deer (McLoughlin et al. 2007).

We observed that survival of fawns was positively affected by avoidance of bed sites with higher light penetration at younger ages, but at older ages this effect reversed (Fig. 2). This negative effect of light penetration on young fawns confirms the thermoregulation interpretation of this variable, light penetration being negatively related to thermal cover (Cook et al. 2005). The interpretation of the effect of light penetration for older fawns is, however, less clear; thermoregulation cannot explain a positive effect on survival at this age. This age effect is, at least in part, due to the increase in available light penetration for non-surviving fawns; whereas no such change with age occurs for surviving fawns (Fig. 2). The explanation for this change in availability for non-surviving fawn is, however, unclear.

As fawns aged, availability changed of sites with cover for concealment, ground cover and proximity of edges, and for non-surviving fawns the availability of light penetration increased too; this suggests a different use of the home range as the fawn ages. This change in available habitat might be caused by changes in the use of the home range by the mother or by changes in the behavior of the fawn: older fawns are more mobile (Jackson et al. 1972) and thus can have a more important influence on the general location of the bed site within the maternal home range. As could be expected, the availability of variables related to concealment from predators and thermoregulation (i.e., thermal cover and insulation from the ground) became less important as fawns aged, whereas preference for the presence of forage (i.e., edge proximity) increased.

Our study examined bed-site selection by roe deer fawns and the effect of bed sites on survival at two spatial scales: small-scale selection by the fawn and the large-scale availability of sites within the maternal home range. We showed that fawn survival was influenced more by the availability of good habitat within the maternal home range than by the bed-site selection by the fawn itself. This is in line with both a recent study on roe deer in another population, which showed that fawn survival highly depends on the availability of preferred plant species within the maternal home range (Pettorelli et al. 2005), and a previous analysis in the focal population that reported a marked positive influence of availability of meadows and road allowance at the scale of the spring-summer maternal home range on reproductive success, and thereby on fawn survival (McLoughlin et al. 2007). However, survival of young fawns appeared to be positively affected by the avoidance of light penetration (i.e., selection for thermal cover). Good home ranges have a close proximity to edges with forage. Although we did not find a strong relationship with their survival, roe deer fawns show selectivity in their bed sites. They selected sites offering concealment, corresponding with a ghost of predation past interpretation, higher light penetration and avoided signs of wild boar activity. The avoidance of light penetration by young fawns supports a thermoregulation interpretation; the selection for it by older surviving fawns remains unclear. The stronger selection for concealment we found was due to a decrease in availability with age, indicating a change in home range use with the age of the fawn. The different home range use as fawns aged was also evident for ground cover and proximity towards edges. Whether such different home range use is caused by changes in behavior of the mother or the increased mobility of the fawn invites further investigation.

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