ANIMAL BEHAVIOUR, 2008, 76, 611–618
doi:10.1016/j.anbehav.2008.03.012

Available online at www.sciencedirect.com
ScienceDirect

Hunting increases vigilance levels in roe deer and modifies feeding site selection

SARAH BENHAIEM, MARION DELON, BRUNO LOURTET, BRUNO CARGNELUTTI, STEPHANE AULAGNIER, A. J. MARK HEWISON, NICOLAS MORELLET & HELENE VERHEYDEN
INRA–CEFS, CRA Toulouse, Castanet Tolosan

(Received 20 December 2007; initial acceptance 13 February 2008; final acceptance 7 March 2008; published online 10 June 2008; MS. number: D-07-20040)

The mortality risk from hunting/predation should increase animals' vigilance and modify their selection of feeding sites. This risk may thus be costly if vigilance interferes with feeding and/or if animals select poorer but safer feeding sites. We observed the vigilance behaviour of roe deer, *Capreolus capreolus*, feeding in a fragmented landscape during and outside the hunting season and compared food availability and local landscape features at these feeding sites with random paired sites. Roe deer spent more time vigilant during the hunting season than outside it. During the hunting season, vigilance decreased as the woodland extent within an 800 m radius increased, but this was not the case outside the hunting season. Vigilance decreased with increasing distance to houses, both during and outside the hunting season. When food is abundant, interference with feeding may be low because animals can simultaneously process food (chewing) and be vigilant. During the hunting season, the total time spent vigilant while chewing increased with increasing food abundance to a lesser extent than outside the hunting season, suggesting a higher level of costly exclusive vigilance during the hunting season. Outside the hunting season animals selected feeding sites that provided more food, but during the hunting season, as risk (proximity to houses) was positively correlated with food availability, animals no longer selected feeding sites on the basis of food availability. Taken together, our results indicate that roe deer trade off risk avoidance for food availability in hunted populations.

Keywords: antipredator behaviour; *Capreolus capreolus*; ecology of fear; feeding behaviour; foraging; landscape; roe deer; trade-off; ungulate

Hunting and predation risks may have indirect nonlethal effects on the behaviour of animals that may be even more important than lethal ones (Brown et al. 1999). The concept of the 'ecology of fear' (Brown et al. 1999) considers the behavioural responses of prey to stress and fear caused by predators and the consequences in terms of fitness. Both the responses and the consequences of hunting/predation are hypothesized to vary across the landscape because risk is related to habitat structure ('the landscape of fear' Brown et al. 1999).

Vigilance plays a major role in the detection of predators (Hopewell et al. 2005). This antipredator behaviour mostly occurs during feeding periods (Whittingham et al. 2004; Lung & Childress 2007) and is widely used (Elgar 1989), potentially increasing fitness by decreasing the risk of mortality (Lima 1998b; Watson et al. 2007). However, as it occurs at the expense of searching for and processing food (Underwood 1982), it may reduce intake rate (Illius & Fitzgibbon 1994), which should also induce long-term costs on fitness (Lima 1998a). However, herbivores can reduce the costs of vigilance if they process food (chew) during vigilance bouts. This is possible when food is concentrated in space and unconcealed (Illius & Fitzgibbon 1994), allowing herbivores to spend less time finding the next bite than chewing the previous one (process 3 in Spalinger & Hobbs 1992). Hence, they benefit from some 'spare time' that can be used for vigilance while chewing. This cost-free vigilance increases with increasing food density because bite size, and thus chewing duration, also increases. Fortin et al. (2004) reported that only a small fraction of this 'spare time' was used for vigilance by bison, *Bison bison*, and wapiti, *Cervus*

Correspondence: H. Verheyden, INRA, UR035, Comportement et Ecologie de la Faune Sauvage, CRA Toulouse, BP 52627, 31326 Castanet-Tolosan Cedex, France (email: Helene.Verheyden@toulouse.inra.fr).

0003–3472/08/$34.00/0

canadensis. Animals may often need to perform more active vigilance in response to external stimuli, notably when risk is high (Pelosse 1976; Fortin et al. 2004). This induced vigilance necessitates the interruption of chewing and the disruption of the ingestion process (Blanchard & Fritz 2007). As a consequence, the costs of vigilance in terms of feeding efficiency should be linked to the proportion of cost-free vigilance (while chewing) relative to the proportion of 'costly' induced (exclusive) vigilance.

Optimal foraging theories (MacArthur & Pianka 1966; Charnov 1976) predict that animals should select feeding sites in a way that maximizes their energetic benefits (Cézilly & Benhamou 1996; Kie 1999), but that also takes into account the risk of predation/hunting (Lima & Dill 1990; Brown & Kotler 2004). If food is limited, a positive correlation between food quality or abundance and risk might exist over the landscape because resources at the best feeding sites (secure and food rich) should be depleted first. This situation may lead to a trade-off between food availability and risk avoidance as food-rich sites may be associated with higher mortality risk (Mysterud et al. 1999; Hochman & Kotler 2007). For example, after the reintroduction of wolves, *Canis lupus*, elk, *Cervus elaphus*, abandoned meadows (forage-rich and risky habitats) for forests (forage-poor but more secure habitats; Creel et al. 2005; Hernandèz & Laundré 2005).

We carried out a study on European roe deer, *Capreolus capreolus*, the most abundant ungulate species in Europe with a wide geographical distribution (Linnell et al. 1998). As the roe deer is an income breeder (Andersen et al. 2000), it is especially dependent on a daily intake of high-quality food and should thus be particularly sensitive to risks affecting food intake rate. In most countries, hunting has replaced natural predators as the primary cause of roe deer mortality (Cederlund et al. 1998).

Roe deer show strong behavioural and ecological plasticity (Hewison et al. 1998), inhabiting contrasting environments including agricultural landscapes (Hewison et al. 2001). Risk should vary over the landscape (Altendorf et al. 2001; Brown & Kotler 2004; Hernandèz & Laundré 2005), for example, increasing with increasing distance from the protection of woodland (mule deer, *Odocoileus hemionus*: Altendorf et al. 2001; Nubian ibex, *Capra ibex nubiana*: Hochman & Kotler 2007). Risk should also increase when visibility decreases because of obstruction by topography or shrubs preventing visual detection of predators (sheep, *Ovis aries*: Hopewell et al. 2005; African antelopes: Underwood 1982; starlings, *Sturnus vulgaris*: Devereux et al. 2006). Finally, the risk of encountering a hunter or a dog may increase with the proximity to human habitation (Frair et al. 2005) and roads (Grover & Thompson 1986).

The aims of our study were (1) to assess how perceived risk as indicated by vigilance behaviour of roe deer is related to landscape features and hunting activity, and (2) to evaluate whether the risk associated with hunting activity interferes with foraging behaviour. We made four predictions.

(1) The time allocated to vigilance should be higher during the hunting season than outside it.

(2) The time allocated to vigilance should increase as a function of certain landscape features: with decreasing woodland extent, with increasing distance to woodland, with decreasing local visibility, and with decreasing distance to roads and houses.

(3) Vigilance should interfere more with feeding during the hunting season (higher overall vigilance and a higher proportion of exclusive vigilance, which is more efficient for detecting predators) than outside it. As a consequence, the proportion of time spent in vigilance while chewing should increase with food abundance to a lesser extent during the hunting season than outside it.

(4) If food abundance is positively correlated with risk over the landscape, roe deer should trade off food availability for risk avoidance leading to lower selection for food-rich feeding sites during the hunting season than outside it.

METHODS

Study Site

We conducted field work from mid-November 2006 to the end of January 2007 (during the hunting season) and from mid-February to the end of March 2007 (outside the hunting season) in the Aurignac district, southwest France (43°13′08″N, 0°52′59″E). The study site (8000 ha) is composed of a mixed landscape with meadows, field crops, small woods, hedges and two larger forest blocks. Woodland occupies 25% of the whole study area, but is locally highly variable. The density of roe deer in 2005 was estimated at around 34 individuals per 100 ha in the central forest block and four to eight individuals per 100 ha in the surrounding fragmented landscape (Hewison et al. 2007). No natural predators of adult roe deer are present, although free-ranging domestic dogs may occasionally kill adults. Red foxes, *Vulpes vulpes*, are present on the study site but can kill only very young fawns. During the 2006–2007 hunting season, hunters killed 125 roe deer using numerous drive beats across the study area.

Behavioural Data Collection

To measure vigilance, we conducted behavioural observations on 88 roe deer (44 during the hunting season and 44 outside) in the open habitat of the fragmented landscape. Eleven different behaviours were identified and recorded: exclusive vigilance (V_e, head raised above shoulder level while scanning surroundings), vigilance while chewing (V_c, vigilance but with chewing), unclassified vigilance (V_u), feeding (collecting food), searching (head bent below shoulder level without collecting food), moving (walking or trotting, head above shoulder level), moving while chewing, grooming, smelling, bedded and 'others'. We observed one individual at a time and we recorded every change of behaviour (focal animal sampling, Altmann 1974) on a tape recorder during feeding phases, at dawn and at dusk, with a telescope (20×80) or binoculars (10×42). When we observed a group, we preferentially focused on the most visible adult from our viewpoint. In a few cases, we were able to observe two or three animals of the same group consecutively. The observers remained hidden