

The Effect of Capture on Ranging Behaviour and Activity of the European Roe Deer *Capreolus capreolus*

Authors: Morellet, Nicolas, Verheyden, H el ene, Angibault, Jean-Marc, Cargnelutti, Bruno, Lourtet, Bruno, et al.

Source: Wildlife Biology, 15(3) : 278-287

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/08-084>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The effect of capture on ranging behaviour and activity of the European roe deer *Capreolus capreolus*

Nicolas Morellet, H el ene Verheyden, Jean-Marc Angibault, Bruno Cargnelutti, Bruno Lourtet & Mark A.J. Hewison

Locating and monitoring animals using tracking devices is a method commonly used for many taxa to study characteristics such as home-range size, habitat selection, movement patterns and other aspects of ranging behaviour. Fitting such devices requires the capture and handling of the study organism and researchers must then assume that a monitored animal behaves in a 'normal' way. We investigated whether the capture and handling of roe deer *Capreolus capreolus* induced behavioural alterations. In particular, we expected that the roe deer would exhibit a 'seeking a refuge and waiting before returning' strategy immediately after release, taking shelter far from the capture scene, in closed habitat, and exhibiting a reduced activity level. We evaluated the effect of capture and handling on 112 roe deer equipped with GPS collars, during a period of 50 days after release. We compared the first 10 days after release with the subsequent days for the following behavioural parameters: distance to the barycentre of their GPS fixes, presence in forest habitat, distance to the nearest forest patch, distance to a source of human disturbance, and activity level. We found pronounced differences in terms of spatial behaviour, habitat use and overall activity level between the two periods in GPS monitored roe deer. We also found differences in terms of spatial displacement between the sexes, with females responding less than males, and among age classes, with yearlings responding most and fawns least, to the capture and handling event. Finally, spatial displacement of roe deer increased with openness of the habitat due, in part, to the scarcity of available shelter in open areas. We conclude that the roe deer exhibited a strategy consisting of seeking a refuge and waiting before returning after capture, handling and fitting of a collar, with displacement towards a refuge habitat, in or near woodland, avoidance of sources of human disturbance and reduced activity levels. From a practical point of view, we recommend removing data during the first days of monitoring as behavioural alterations due to capture and handling may be pronounced.

Key words: *Capreolus capreolus*, capture and handling effects, disturbance, home range, roe deer, shelter, space use, stress, telemetry

Nicolas Morellet, H el ene Verheyden, Jean-Marc Angibault, Bruno Cargnelutti, Bruno Lourtet & Mark A.J. Hewison, *Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, BP 52627, F-31326 Castanet-Tolosan Cedex, France - e-mail addresses: Nicolas.Morellet@toulouse.inra.fr (Nicolas Morellet); Helene-Verheyden@toulouse.inra.fr (Helene Verheyden); Jean-Marc.Angibault@toulouse.inra.fr (Jean-Marc Angibault); Bruno.Cargnelutti@toulouse.inra.fr (Bruno Cargnelutti); Bruno.Lourtet@toulouse.inra.fr (Bruno Lourtet); Mark.Hewison@toulouse.inra.fr (Mark A.J. Hewison)*

Corresponding author: Nicolas Morellet

Received 15 December 2008, accepted 6 May 2009

Associate editor: Atle Mysterud

A wide array of research programmes on live vertebrates requires the capture and handling of the study organism which may cause some mortality or reduction in survival probability due to post-release

shock, trauma and possible behavioural alterations (Haulton et al. 2001). The capture process may induce physiological changes, including elevated heart and respiratory rates, increased body temper-

ature, altered blood and urine characteristics, injuries, capture myopathy and death (Kock et al. 1987, DelGiudice et al. 1990, Marco & Lavin 1999). Indeed, the intrusion into the life of the study organism due to capture and handling is likely to be one of the most stressful events of their lives and can provoke responses that may confound any clear-cut answer to the research question being addressed.

Moberg (2000) defines stress as "the biological response elicited when an individual perceives a threat to its homeostasis". In fact, stress responses are adaptive responses to potentially life-threatening events such as the presence of a predator. However, sometimes stress may result in distress (Moberg 2000), when the animal incurs a biological cost so large that it needs to divert resources away from normal biological functions to cope with this stress factor (threat). This state, also called emergency life history stage, may involve several behaviours such as a fight or flight response, sickness behaviour and fever, and specific behavioural strategies such as seeking a refuge and waiting before returning (see also Wingfield 2005). These behavioural responses are regulated by corticoids that are known to increase drastically following capture and manipulation of animals (DelGiudice et al. 1990, Diverio et al. 1996, Ingram et al. 1999, Montane et al. 2003). Even if behavioural responses elicited by capture stress are most often reversible, they impose energetic costs and trade-off with other vital behaviours and physiological processes (e.g. immunity) that may have subclinical effects and long-term consequences on animal welfare and subsequent survival.

Capture stress may vary among capture techniques (DeNicola & Swihart 1997, Langkilde & Shine 2006). Several authors have studied the effects of capture on mortality (Haulton et al. 2001, DelGiudice et al. 2005), on biological or physiological parameters (Kock et al. 1987, Marco & Lavin 1999, Montané et al. 2002, Bonacic et al. 2006), on injuries (Cattet et al. 2008, Webb et al. 2008), on reproduction (Ramsay & Stirling 1986, Laurenson & Caro 1994, Côté et al. 1998) and on body condition (Ramsay & Stirling 1986, Cattet et al. 2008) of various study species. Short-term behavioural alterations due to handling and capture involve increasing movement (in frog *Litoria lesueuri* (Langkilde & Alford 2002), in skinks *Oligosoma ottagense* (Germano 2007) and in bears *Ursus* sp. (Cattet et al. 2008)), altered mobility (in little bustard *Tetrax tetrax* (Ponjoan et al. 2008)) and reduced food consumption and activity (in red grouse

Lagopus l. scoticus (Boag 1972) and red deer *Cervus elaphus* (Blanc & Brelurut 1997)).

Irrespective of the very real concerns in terms of animal welfare (Veissier & Boissy 2007, Korte et al. 2007), for behavioural data to be informative, it is clearly essential that a monitored animal behaves in a 'typical' or 'normal way'. If our aim is to better understand the ecology of the monitored animal, it is important to understand the potential effects of capture and marking on animal behaviour. Locating and monitoring animals using tracking devices is a method commonly used for many taxa to study characteristics such as home-range size, habitat selection and movement patterns (e.g. Kenward 2001). In order to attach these devices, numerous techniques have been developed for capturing very different species living in contrasting environmental situations (e.g. Wilson et al. 1996). In this context, Laurenson & Caro (1994) called for researchers to determine whether their field techniques have a detrimental effect on the study organisms. To our knowledge, to date no study has evaluated the short term effect of handling and capture on the ranging behaviour of ungulates (but see Moa et al. (2001) on the Eurasian lynx *Lynx lynx* and Ramsay & Stirling (1986) on polar bear *Ursus americanus*). Thus, in our study we investigated whether the capture and handling of roe deer *Capreolus capreolus*, a medium-sized ungulate, modifies its space use, activity and habitat use immediately following release. Specifically, if capture and handling of roe deer is likely to be a stressful event, we expected that the roe deer would express a strategy consisting of seeking a refuge and waiting before returning, taking shelter far from the capture scene in closed habitat, and exhibiting a reduced activity level immediately after release. Some recommendations are provided in order to minimise any negative consequences of this capture effect as a confounding factor when studying ranging behaviour of large herbivores.

Material and methods

Study area

Our study was carried out in a fragmented agricultural landscape of the Aurignac canton (43°13'N, 0°52'E), situated in the Comminges region of southwest France (Hewison et al. 2007). It is a hilly region, rising to a maximum of 380 m a.s.l., which has undergone substantial modification due to intensification of agricultural practice, with a loss of

hedges and copses, the planting of new crop types (corn, sorghum) and an increase in average field size. This has resulted in a mixed landscape of open fields and small woodland patches (average size 3 ha), with a central larger forest of 672 ha. The primary land use is pastoral, for sheep and cattle grazing, although agricultural crops are increasing. The human population is dispersed throughout the site, in small villages and farms distributed along the extensive road network which covers the study site. The climate is oceanic, with an average annual temperature of 11-12°C and 800 mm precipitation, mainly in the form of rain.

The total study area covers around 10,000 ha, about 21% of which is wooded. At present, the landscape is characterised by woodland patches (14% of the area) dominated by oak *Quercus* spp., and a central forest (7% of the area) containing a mixed species forest of Douglas-fir *Pseudotsuga menziesii* and oak. Meadows, cultivated fields and hedges cover about 34, 33 and 7% of the total area, respectively (see Hewison et al. in press for more details).

The roe deer population is hunted on a regular basis by stalking (bucks only) during summer (June-August) and by drive hunts with dogs during autumn-winter (September - January). The hunting teams are organised in relation to the boundaries of one, or a few, communes. Deer density in the central forest was estimated at around 34 deer/100 ha in the winter of 2005, while density in the surrounding fragmented landscape was between 4 and 8 deer/100 ha (Hewison et al. 2007).

Study population and data collection

From 2002 to 2008, roe deer were caught during winter (16 November - 27 March) using large-scale drives of between 30 and 100 beaters and up to 4 km of long-nets positioned at one of 10 capture sites. When a roe deer was caught in the net, at least two persons were needed to remove the animal from the net and transfer it to a box (a wooden retention box, providing darkness and ventilation, but a minimum

of space to impede injuries and limit stress) over a period of a few minutes (in general < 10 minutes). At the end of the capture event, all boxes were collected in a central place on the capture site for marking, generally using a car to transport the roe deer. Finally, just before release from the marking site, roe deer were handled a second time to record specific information and equip them with a radio-collar. This phase lasted for approximately 10 minutes during which we recorded body weight, sex and hind foot length, and attributed an age class to the animal. Juveniles (<1 year old) were distinguished from older deer on the basis of presence of a tri-cuspid third pre-molar milk tooth (Ratcliffe & Mayle 1992). For older deer, we used tooth wear to distinguish yearlings (18 months old) from adults of > 2 years of age. We then equipped deer with ear tags and radio-collars with a 12 channel Lotek 3300 GPS (for home-range and habitat use studies) and released them from the site. The total time from capture to release lasted several hours (i.e. 115 to 416 minutes in 2009, not measured previously). Altogether, 112 roe deer were monitored (Table 1) and equipped with collars weighing 385 g, or about 1.7, 1.9 and 2.4% of body mass for adults, yearlings and fawns, respectively (range: 1.3-2.2% for adults, 1.7-2.3% for yearlings and 1.9-4.0% for fawns). Collars were programmed to obtain the location of the roe deer with a schedule of one GPS fix every four hours (during the first two winters) or every six hours (during the following winters). We performed differential correction in order to improve fix accuracy (Adrados et al. 2002), and 50% of the fix locations were located within 14 m of their true position in our study area (Cargnelutti et al. 2007). All fixes (i.e. latitude and longitude) were converted to Lambert III coordinates using pathfinder Office version 2.7 (Trimble navigation Ltd, USA).

Statistical analysis

The 10 capture sites were grouped into three landscape units (sectors) based on contrasting land-

Table 1. Mean length of time (in months; \pm SE) by year, sex and age class during which individual roe deer were monitored (with the sample size given in brackets).

Year	Female			Male			Total
	Adults	Yearlings	Fawns	Adults	Yearlings	Fawns	
2003	11.1 \pm 0.7 (6)	9.1 (1)	9.7 \pm 1.2 (5)	10.3 \pm 0.9 (7)		8 \pm 1.2 (3)	10 \pm 1 (22)
2004	3.6 (1)	10.8 (1)	10 \pm 1.2 (2)	12.3 (1)		8.6 \pm 1.1 (5)	8.9 \pm 1.3 (10)
2005	11.0 \pm 0.4 (11)	11.5 \pm 0.1 (2)	9 \pm 1.5 (5)	10 \pm 0.9 (7)	9.3 \pm 1.2 (3)	9.8 \pm 1.3 (5)	10.2 \pm 0.9 (33)
2006	10.9 \pm 0.4 (10)	11 \pm 0.1 (2)		10.9 \pm 0.5 (11)	11.2 (1)	11.2 (1)	10.9 \pm 0.4 (25)
2007	10.1 \pm 0.8 (11)	10.8 (1)	10.7 \pm 0.2 (4)	10.5 (1)		9.7 \pm 1 (5)	10.1 \pm 0.7 (22)

scape structure in terms of woodland extent and the relative proportions of meadows and cultivated fields (Hewison et al. in press). Thus, we identified three sectors of contrasting landscape structure: a forest block (sector 1 with 100% woodland), a partially wooded area (sector 2 with 35% woodland, 38.5% meadows, 21.6% cultivated fields and 2.1% hedgerows) and an open agricultural area with highly fragmented woodland (sector 3 with 12.5% woodland, 33.8% meadows, 42.7% cultivated fields and 6.3% hedgerows).

Our initial aim was to determine the effect of capture on the ranging behaviour of the roe deer in the aftermath of the capture event. We considered three indirect ways to measure this effect: in terms of any brief spatial displacement of the home range, any modification of habitat use or, finally, any alteration in activity level. To study the immediate, short-term effects of capture on the spatial behaviour of roe deer, we considered the first 50 days of monitoring of each animal. We chose 50 days because after this period (ending the 3 May, 24 March and 9 April for the latest capture date of adults, yearlings and fawns, respectively), spatial behaviour of roe deer may change due to the onset of territoriality and the dispersal of yearlings (Linnell et al. 1998). For each individual, we calculated the barycentre of all GPS fixes and then measured the Euclidean distance of each fix to this barycentre. Under the hypothesis of no disturbance due to capture, there should be no relationship between the mean distance to the barycentre and the time (number of days) after release. Alternatively, an animal may need several days before it exhibits 'normal' ranging behaviour which we assumed to be similar to its behaviour prior to the capture itself. We used generalised additive mixed models (Wood 2006) to investigate variation in distance to the barycentre over time after release with a smoother (i.e. a spline), including the period (two modalities), sex (two modalities), landscape sector (three modalities) and age class (three modalities) as factors and the individual's home-range size as a covariable, with the individual identifier as a random effect. Time after release was calculated in hours but expressed in days. We used a smoother in the statistical approach to control for the temporal correlation of successive fixes. We divided the 50 days of monitoring into two periods, the first 10 days after release (period 1) and the following 40 days (period 2) and compared spatial displacement between periods. White & Garrott (1990) recommended taking into account "sev-

eral days or up to one week for newly instrumented animals to acclimate to the transmitter". We defined the length of the first period in relation to the pattern of spatial displacement revealed by the smoothing approach (Fig. 1A). We also performed the same model for each individual separately and looked for the point when the distance to the barycentre was lower than the mean distance across the 50-days. This generally occurred within the 10-day period (7.39 ± 0.701 days) and thus confirmed the relevance of the choice of 10 days for defining the first post-capture period. We used a total study period of 50 days in order to obtain a representative estimate of the barycentre which was not overly influenced by the first fixes post capture, since these may be influenced by the capture event itself. Hence, because of these constraints, period 2 covered a longer time interval (40 days) than period 1. Moreover, because we hypothesised that the effect of capture might differ between sectors, sexes and age classes, we considered the two-way interactions of these three factors with period. Finally, because home-range size increases with landscape openness in roe deer (Cargnelutti et al. 2002), we included home-range size (calculated for period 2, using the kernel method at 95%) in the model as a covariable to control for this effect. To test the statistical significance of the different effects in the model, we used the likelihood ratio test derived from the models with and without a given effect (Pinheiro & Bates 2000).

To test for a possible modification in habitat use and activity pattern due to post-capture stress, we compared the relevant variables between the two periods, as before. However, for this part of the analysis, we considered periods of equal length (i.e. 10 days for each of the periods 1 and 2) so that for these analyses we retained fixes for the first 20 days after release only, in order to have the same sample size for the two periods. To test whether animals modify their habitat use post capture, we compared the percentage of fixes inside forest habitat (P) between the two periods with a paired t-test using the arc sine square root of the proportion. We also compared the mean distance of fixes to the nearest forest patch and the mean distance of fixes to the nearest source of human disturbance between these two periods using paired t-tests. For sources of human disturbance, we used a proxy based on the average of the distance to the nearest road and the distance to the nearest house for each fix. We also considered the abundance of roads and houses in the individual home ranges but did not use them

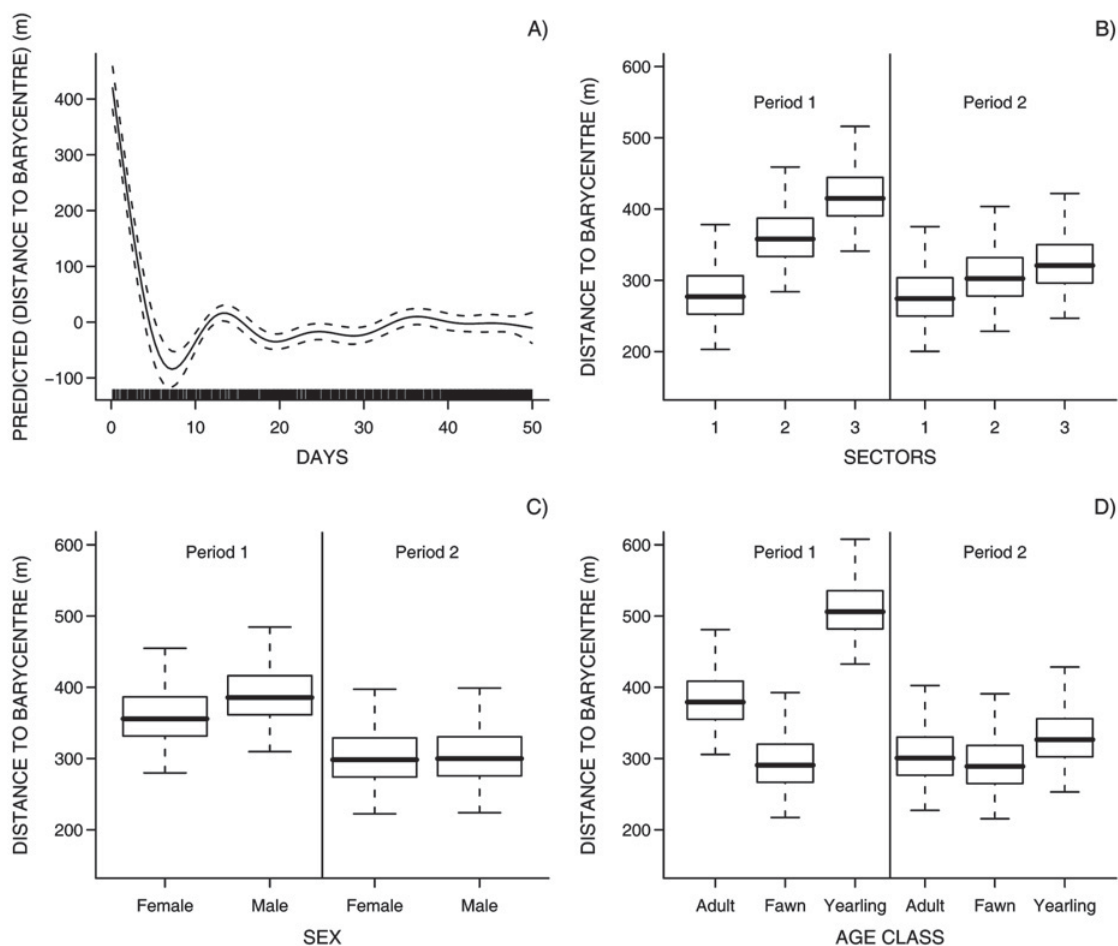


Figure 1. Individual distances between GPS fixes and the barycentre of their fixes over the first 50 days predicted by the most-supported generalised additive mixed model for 112 roe deer (including the individual as a random effect): as a function of time after release, including a smoothing effect with a spline (A), the two-way interaction between period and sector of capture (B), the two-way interaction between period and sex (C) and the two-way interaction between period and age class (D). In this most-supported model, we controlled for home-range size (calculated over the 50 days, with the kernel method at 95%) to be able to compare contrasting situations. Each two-way interaction is plotted while controlling for other significant factors.

in the analysis as many home ranges of this study did not physically include these components (although they were not far in terms of absolute distances). We do, however, believe that the distance to the closest road or closest house gives a better idea of the level of human disturbance in the vicinity of the home range, as we have, for example, shown elsewhere that the vigilance of roe deer decreases with increasing distance to the nearest house, in the same study area (Benhaïem et al. 2008).

In terms of monitoring activity patterns, the GPS collar records movements of the collar with an activity sensor (Lotek 2002). A dual axis motion sensor records 'up-down' and 'side-to-side' movements of the head and the neck, respectively; the X and Y

sensors. Another sensor, an HD sensor, computes the proportion of time that the head is in a downward position. These three measures were recorded every five minutes. For the X and Y sensors, a given value represents the number of contacts in the two perpendicular directions over the previous 5-minute period, with a maximal count value of 255. The HD sensor records as a percentage. We summed the activity values for the two different periods and then reduced the number of activity variables by considering the first factorial axis of a principal component analysis (PCA) of these three variables (Dolédéc & Chessel 1991). To compare the overall activity level between periods, indexed by the first factorial axis of the PCA, we used a paired t-test.

Results

All the two-way interactions, i.e. age class*period (LR = 86.75, df = 2, N = 112, $P < 0.0001$), sex*period (LR = 18.27, df = 1, N = 112, $P < 0.0001$) and sector*period (LR = 49.62, df = 2, N = 112, $P < 0.0001$) explained a significant proportion of the variance in the model of distance to the barycentre. Home-range size (LR = 164.95, df = 1, N = 112, $P < 0.0001$) and time after release (LR = 779.06, df = 2, N = 112, $P < 0.0001$) also explained significant variation in this model. Distance to the barycentre increased linearly with home-range size (slope = 0.86 ± 0.04). Regarding time after release (see Fig. 1A), there was a sharp decrease in the distance to the barycentre during the first 10 days, but this levelled out at around zero metres, with no further discernible pattern ($F = 90.52$, df = 8.87, $P < 0.0001$). Thus, roe deer were located farther from their normal home range during the first period compared to the second period, revealing a clear post-capture displacement of the home range. However, this general pattern varied between sectors, sexes and age classes (see Figs. 1B-D, respectively). The degree of difference between periods 1 and 2 in distance to the barycentre decreased with increasing woodland extent, from sector 3 to sector 1 (see Fig. 1B) revealing that roe deer show less post-capture displacement in forested compared to open landscapes. The degree of difference between periods 1 and 2 in distance to the barycentre was more pronounced in males than in females (see Fig. 1C). Finally, the degree of difference between periods 1 and 2 in distance to the barycentre was more pronounced in yearlings than in fawns, while adult roe deer showed an intermediate position between these two values (see Fig. 1D). This model accounted for 27.6% of the total variability.

Regarding the possible alteration of habitat use due to capture, the roe deer used forest habitat more during the first period than during the second one ($P_1 = 57.5\% \pm 3.11$ and $P_2 = 49.1\% \pm 3.31$, $t = 4.62$, df = 111, $P < 0.0001$). Similarly, the mean distance to the nearest forest (DF) patch was significantly lower ($DF_1 = 50.9 \text{ m} \pm 5.66$ and $DF_2 = 63.6 \text{ m} \pm 6.68$, $t = 3.10$, df = 111, $P = 0.0024$), and the mean distance to the nearest source of human disturbance (DHD) was significantly higher ($DHD_1 = 343.2 \text{ m} \pm 20.75$ and $DHD_2 = 325.4 \text{ m} \pm 20.87$, $t = -2.68$, df = 111, $P = 0.0085$) during the first period than during the second period. Thus, roe deer used forest habitat significantly more, remaining closer to forest cover

and further from sources of human disturbance, in the first days immediately following capture compared to later on.

As we did not record activity data for the first years of monitoring (2002-2003), we analysed sensor data for only 92 of the 112 roe deer. The first axis of the PCA of the sensor data explained 50% of the variability. The X and Y sensors were more highly correlated with this axis than the HD sensor (coefficients = 0.84, 0.85 and 0.26 for X, Y and HD sensors, respectively). The average value of the first factorial axis describing overall activity level was significantly lower during period 1 than during period 2 ($t = 5.65$, df = 91, $P < 0.0001$), indicating that activity levels were lower in period 1 than in period 2.

Discussion

We found pronounced differences in terms of spatial behaviour, habitat use and overall activity level between the first period of 10 days after release and the following days in GPS monitored roe deer. Roe deer show a strategy consisting of seeking a refuge and waiting before returning in response to capture, handling and fitting of a collar, with displacement towards a refuge (near or in woodland, far from sources of human disturbance) and a reduction in activity level. Immediately following capture, roe deer were located further from the centre of their home range than normal. This displacement of the home range was more pronounced among yearlings than among adults and fawns. Adult roe deer are considered to have a high degree of spatial stability whereas yearlings are generally more mobile, using a larger daily and seasonal range (Hewison et al. 1998). Yearlings may enlarge their home range in order to explore new habitats before settling within a defined home range or territory (Van Moorter et al. 2008), or alternatively their higher mobility may be due in part to the fact that they suffer more aggressive interactions than adults (e.g. Wahlström 1994). Thus, yearlings may express a more pronounced response to the capture process either because of their inherent lack of spatial stability or due to their greater level of basal stress. However, younger animals are known to be able to learn and adapt more easily, and tend to be less stressed by disturbance in general (Lansade et al. 2007). The fact that capture and handling appeared to have the least impact on fawns' ranging behaviour is in agreement with the prediction of lower stress levels

among young animals. However, we cannot be absolutely sure that the absence of a marked effect on the behaviour of fawns was real, as we have to consider that roe deer fawns are not really independent from their mother during their first winter (Linnell et al. 1998). As we were only rarely able to simultaneously monitor mother-fawn couples, it seems likely that this apparent lower level of response among fawns was due to the fact that the fawns' mothers were generally not caught in the same capture operation and hence the fawn's stress response was attenuated by the presence of its non-stressed mother.

Roe deer of different sex reacted differently to the capture and handling process. Males seemed to be more sensitive, showing a greater displacement of their home range immediately after release compared to their normal range. Roe deer males are considered strongly seasonally territorial (Bramley 1970), but during winter (the capture season) are non-territorial. Moreover, males are solitary, and do not exhibit strong social bonds with their fawns or other conspecifics (Hewison et al. 1998). In contrast, the vast majority of females have fawns at heel, even though by this period fawns should be able to survive without their mother as roe deer are already weaned by winter (Sempéré et al. 1988). One explanation of this apparent sexual difference in post-capture ranging behaviour may therefore be linked to this difference in social environment. Contrary to males, females do have social ties to their fawns, and potentially to young from previous years, forming maternal clans (Hewison et al. 1998). Hence, females may return relatively quickly to their normal home range to reestablish these bonds.

Finally, we found a pronounced effect of landscape structure on the degree of post-capture home-range displacement. Displacement in response to capture increased with the openness of the habitat. First we should note that, during capture operations, roe deer tend to run over greater distances immediately prior to capture in more open areas. Indeed, animals are more exposed (e.g. to potential predators and disturbance) in open areas and are able to detect human presence from a greater distance than they can in closed habitats (Benhaïem et al. 2008). The roe deer is predominantly a species of closed, generally wooded, habitats which provide both resources and shelter. Indeed, closed undisturbed habitats appear to be a vital requirement for the species (Tufto et al. 1996). During winter, in more open cultivated areas, sheltered habitats (gen-

erally, wooded patches) are more dispersed over the landscape as cultivated fields provide no shelter for roe deer at this time of year. Thus, if roe deer need to take shelter in a closed habitat immediately after release, this may explain the relationship between the level of displacement and the level of habitat openness. This pattern was not due to home-range size, which increases with habitat openness (Cargnelutti et al. 2002), as we controlled for this effect in the analysis. In support of this, we found that, immediately following release, the use of forest habitat by the roe deer was higher than during subsequent ranging activity. This suggests that the impact and associated stress of the capture and handling process induced deer to seek shelter, either inside or in the vicinity of closed forest habitat and far from potential sources of human disturbance. Moreover, we observed that this pronounced behavioural response appeared to continue for a period of at least one week. Similarly, Moa et al. (2001) found a possible stress response linked with the capture event, in that a longer period elapsed before lynx returned to their catch site than to random sites.

In our study, the stress of the capture process also induced a reduction in the overall level of activity of roe deer. This type of effect has also been observed on captive red grouse *Lagopus lagopus scoticus* (Boag 1972). The fact that roe deer reduced their level of activity immediately after release may have some non-negligible consequences for the acquisition of resources, as has also been observed directly on red grouse (Boag 1972) and indirectly on mallard *Anas platyrhynchos* and blue-winged teal *Anas discors* (Greenwood & Sargeant 1973). Indeed, mallards equipped with radio-packs lost considerably more weight than did controls during the first weeks after capture and attachment of the radio-packs (Greenwood & Sargeant 1973). However, a study of Gilmer et al. (1974) on mallard and wood ducks *Aix sponsa* concluded that the capture and handling of ducks did not seriously affect the data collected on movements and habitat use. Cattet et al. (2008) found a reduction in movement after capture and of body condition following repeated captures of bears. Concerning ungulates, few data are available, but Blanc & Brelurut (1997) found a decrease of 40% in grazing activity of red deer hinds over a short period of eight days after fitting of a GPS-collar (see also Cousse & Janeau 1991). Roe deer are generally considered income breeders (*sensu* Jönsson (1997)), stocking few fat reserves (Hewi-

son et al. 1996), relying instead on daily energy intake to offset the costs of reproduction. The reduction of activity and change of habitat use that we observed in roe deer likely resulted in a reduction in food intake. Thus, a temporary nutritional stress may occur at this time, in addition to the stress of being captured and fitted with a collar. This could potentially have a detrimental long-term impact for roe deer in some situations, due to their low levels of reserves for offsetting any additional costs imposed by capture stress.

Finally, the capture of wild animals is not a negligible source of disturbance and, from a practical point of view, we recommend that researchers remove data from the initial post-release monitoring period, the first week in our case, before performing data analyses on ranging behaviour of their subject animals. In our case, considering all the fixes available during the first 50 days after release to estimate home-range size (with the kernel method at 95%) increased the range size by 26% in comparison with the same estimation without the first 10 days after release (and by 52.5% for a kernel at 100%). In this regard, White & Garrott (1990) recommended considering a period of acclimatisation before collecting data which should be considered as indicative of normal behaviour. In this paper, we showed that capture and handling induced behavioural alterations when comparing the first 10 days after release with subsequent monitoring in GPS monitored roe deer. Thus, we caution scientists using GPS or VHF collars to study space use, activity and habitat use, that behavioural alterations due to capture and handling are likely a general phenomenon. However, in the context of this comparison, we assumed that animals recovered their normal spatial behaviour within a relatively short period of time (a few days). Whether animals carrying collars ever behave in a 'normal' fashion, compared to their behaviour pre-capture, is clearly difficult to demonstrate and is a necessarily common assumption which must be considered when studying the behaviour of wild animals.

Acknowledgements - we would like to thank J.P. Chanal and the local hunting associations with the Fédération Départementale des Chasseurs de la Haute Garonne for allowing us to work in the central forest and the surrounding fragmented area, respectively, as well as numerous co-workers and volunteers for their assistance. We thank two anonymous referees for constructive criticism of an earlier draft of this manuscript.

References

- Adrados, C., Girard, I., Gendner, J-P. & Janeau, G. 2002: GPS location accuracy improvement due to selective availability removal. - *Comptes Rendus Biologies* 325: 1-6.
- Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M., Morellet, N. & Verheyden, H. 2008: Hunting increases vigilance levels in roe deer and modifies feeding site selection. - *Animal Behaviour* 76: 611-618.
- Blanc, F. & Brelurut, A. 1997: Short-term behavioral effects of equipping red deer hinds with a tracking collar. - *Zeitschrift für Säugetierkunde-International Journal of Mammalian Biology* 62: 18-26.
- Boag, D.A. 1972: Effect of radio packages on behavior of captive red grouse. - *Journal of Wildlife Management* 36: 511-518.
- Bonacic, C., Feber, R.E. & Macdonald, D.W. 2006: Capture of the vicuna (*Vicugna vicugna*) for sustainable use: Animal welfare implications. - *Biological Conservation* 129: 543-550.
- Bramley, P.S. 1970: Territoriality and reproductive behaviour of roe deer. - *Journal of Reproduction and Fertility Supplement* 11: 43-70.
- Cargnelutti, B., Coulon, A., Hewison, A.J.M., Goulard, M., Angibault, J-M. & Morellet, N. 2007: Testing GPS performance for wildlife monitoring using mobile collars with known reference points. - *Journal of Wildlife Management* 71: 1380-1387.
- Cargnelutti, B., Reby, D., Desneux, L., Angibault, J-M., Joachim, J. & Hewison, A.J.M. 2002: Space use by roe deer in a fragmented landscape some preliminary results. - *Revue d'Ecologie - La Terre et la Vie* 57: 29-37.
- Cattet, M., Boulanger, J., Stenhouse, G., Powell, R.A. & Reynolds-Hogland, M.L. 2008: An evaluation of long-term capture effects in ursids: Implications for wildlife welfare and research. - *Journal of Mammalogy* 89: 973-990.
- Côté, S.D., Festa-Bianchet, M. & Fournier, F. 1998: Life-history effects of chemical immobilization and radio-collars on mountain goats. - *Journal of Wildlife Management* 62: 745-752.
- Cousse, S. & Janeau, G. 1991: Conséquences de la capture et du marquage sur le comportement individuel et social des ongulés sauvages. - *Gibier Faune Sauvage* 8: 127-139. (In French).
- DelGiudice, G.D., Kunkel, K.E., Mech, L.D. & Seal, U.S. 1990: Minimizing capture-related stress on white-tailed deer with a capture collar. - *Journal of Wildlife Management* 54: 299-303.
- DelGiudice, G.D., Sampson, B.A., Kuehn, D.W., Powell, M.C. & Fieberg, J. 2005: Understanding margins of safe capture, chemical immobilization, and handling of free-ranging white-tailed deer. - *Wildlife Society Bulletin* 33: 677-687.

- DeNicola, A.J. & Swihart, R.K. 1997: Capture-induced stress in white-tailed deer. - *Wildlife Society Bulletin* 25: 500-503.
- Diverio, S., Goddard, P.J. & Gordon, I.J. 1996: Use of long-acting neuroleptics to reduce the stress response to management practices in red deer. - *Applied Animal Behaviour Science* 49: 83-88.
- Dolédec, S. & Chessel, D. 1991: Recent developments in linear ordination methods for environmental sciences. - *Advances in Ecology* 1: 133-155.
- Germano, J.M. 2007: Movements, home ranges, and capture effect of the endangered Otago Skink (*Oligosoma ottagense*). - *Journal of Herpetology* 41: 179-186.
- Gilmer, D.S., Ball, I.J., Cowardin, L.M. & Riechmann, J.H. 1974: Effects of radio packages on wild ducks. - *Journal of Wildlife Management* 38: 243-252.
- Greenwood, R.J. & Sargeant, A.B. 1973: Influence of radio packs on captive mallards and blue-winged teal. - *Journal of Wildlife Management* 37: 3-9.
- Haulton, S.M., Porter, W.F. & Rudolph, B.A. 2001: Evaluating 4 methods to capture white-tailed deer. - *Wildlife Society Bulletin* 29: 255-264.
- Hewison, A.J.M., Angibault, J-M., Boutin, J-M., Bideau, E., Vincent, J-P. & Sempere, A. 1996: Annual variation in body composition of roe deer (*Capreolus capreolus*) in moderate environmental conditions. - *Canadian Journal of Zoology* 74: 245-253.
- Hewison, A.J.M., Angibault, J-M., Cargnelutti, B., Coulon, A., Rames, J-L., Serrano, E., Verheyden, H. & Morellet, N. 2007: Using radio-tracking and direct observation to estimate roe deer *Capreolus capreolus* density in a fragmented landscape - a pilot study. - *Wildlife Biology* 13(3): 313-320.
- Hewison, A.J.M., Morellet, N., Verheyden, H., Dautresne, T., Angibault, J-M., Cargnelutti, B., Merlet, J., Picot, D., Rames, J-L., Joachim, J., Lourtet, B., Serrano, E., Bideau, E. & Cebe, N. in press: Landscape fragmentation influences winter body mass of roe deer. - *Ecography*.
- Hewison, A.J.M., Vincent, J-P. & Reby, D. 1998: Social organisation of European roe deer. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp. 189-219.
- Ingram, J.R., Crockford, J.N. & Matthews, L.R. 1999: Ultradian, circadian and seasonal rhythms in cortisol secretion and adrenal responsiveness to ACTH and yarding in unrestrained red deer (*Cervus elaphus*) stags. - *Journal of Endocrinology* 162: 289-300.
- Jönsson, K.I. 1997: Capital and income breeding as alternative tactics of resource use in reproduction. - *Oikos* 78: 57-66.
- Kenward, R.E. 2001: *A Manual for Wildlife Radio Tagging*. - Academic Press, London, 311 pp.
- Kock, M.D., Clark, R.K., Franti, C.E., Jessup, D.A. & Wehausen, J.D. 1987: Effects of capture methods on biological parameters in free-ranging bighorn sheep (*Ovis canadensis*): evaluation of normal, stressed and mortality outcomes and documentation of postcapture survival. - *Journal of Wildlife Diseases* 23: 652-662.
- Korte, S.M., Olivier, B. & Koolhaas, J.M. 2007: A new animal welfare concept based on allostasis. - *Physiology & Behavior* 92: 422-428.
- Langkilde, T. & Alford, R.A. 2002: The tail wags the frog: Harmonic radar transponders affect movement behavior in *Litoria lesueuri*. - *Journal of Herpetology* 36: 711-715.
- Langkilde, T. & Shine, R. 2006: How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. - *Journal of Experimental Biology* 209: 1035-1043.
- Lansade, L., Bouissou, M.F. & Boivin, X. 2007: Temperament in preweanling horses: Development of reactions to humans and novelty, and startle responses. - *Developmental Psychobiology* 49: 501-513.
- Laurenson, M.K. & Caro, T.M. 1994: Monitoring the Effects of Nontrivial Handling in Free-Living Cheetahs. - *Animal Behaviour* 47: 547-557.
- Linnell, J.D.C., Wahlström, L.K. & Gaillard, J-M. 1998: From birth to independence: Birth, growth, neonatal mortality, hiding behaviour and dispersal. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); *The European roe deer: The biology of success*. Scandinavian University Press, Oslo, pp. 257-283.
- Lotek 2002: Small and midsize animals GPS location system user's manual, GPS_3300, 48 pp.
- Marco, I. & Lavin, S. 1999: Effect of the method of capture on the haematology and blood chemistry of red deer (*Cervus elaphus*). - *Research in Veterinary Science* 66: 81-84.
- Moa, P., Negard, A., Overskaug, K. & Kvam, T. 2001: Possible effects of the capture event on subsequent space use of Eurasian lynx. - *Wildlife Society Bulletin* 29: 86-90.
- Moberg, G.P. 2000: Biological responses to stress: implications for animal welfare. - In: Moberg, G.P. & Mench, J.A. (Eds.); *The biology of animal stress: Basic principles and implications for animal welfare*. CAB International, Wallingford, pp. 1-21.
- Montané, J., Marco, I., Lopez-Olivera, J., Perpignan, D., Manteca, X. & Lavin, S. 2003: Effects of acepromazine on capture stress in roe deer (*Capreolus capreolus*). - *Journal of Wildlife Diseases* 39: 375-386.
- Montané, J., Marco, I., Manteca, X., Lopez, J. & Lavin, S. 2002: Delayed acute capture myopathy in three roe deer. - *Journal of Veterinary Medicine Series a - Physiology Pathology Clinical Medicine* 49: 93-98.
- Pinheiro, J.C. & Bates, D.M. 2000: *Mixed effects Models in S and S-PLUS*. - Springer, New-York, 528 pp.
- Ponjoan, A., Bota, G., De La Morena, E.L.G., Morales, M.B., Wolff, A., Marco, I. & Manosa, S. 2008: Adverse

- effects of capture and handling little bustard. - *Journal of Wildlife Management* 72: 315-319.
- Ramsay, M.A. & Stirling, I. 1986: Long-term effects of drugging and handling free-ranging polar bears. - *Journal of Wildlife Management* 50: 619-626.
- Ratcliffe, P.R. & Mayle, B.A. 1992: Roe deer biology and management. - Forestry Commission Bulletin 105. HMSO, London, UK, 28 pp.
- Sempéré, A.J., Noel, A.M. & Boutin, J-M. 1988: Etude comparative de l'influence des variations saisonnières de la progestéronémie et de la lactation sur le développement des tétines chez le chevreuil. - *Gibier Faune Sauvage* 5: 331-343. (In French).
- Tufto, J., Andersen, R. & Linnell, J.D.C. 1996: Habitat use and ecological correlates of home range size in a small cervid: the roe deer. - *Journal of Animal Ecology* 65: 715-724.
- Van Moorter, B., Gaillard, J-M., Hewison, A.J.M., Said, S., Coulon, A., Delorme, D., Widmer, O., Cargnelutti, B. & Angibault, J-M. 2008: Evidence for exploration behaviour in young roe deer (*Capreolus capreolus*) prior to dispersal. - *Ethology Ecology & Evolution* 20: 1-15.
- Veissier, I. & Boissy, A. 2007: Stress and welfare: Two complementary concepts that are intrinsically related to the animal's point of view. - *Physiology & Behavior* 92: 429-433.
- Wahlström, L.K. 1994: The significance of male-male aggression for yearling dispersal in roe deer (*Capreolus capreolus*). - *Behaviour Ecology and Sociobiology* 35: 409-412.
- Webb, S.L., Lewis, J.S., Hewitt, D.G., Hellickson, M.W. & Bryant, F.C. 2008: Assessing the helicopter and net gun as a capture technique for white-tailed deer. - *Journal of Wildlife Management* 72: 310-314.
- White, G.C. & Garrott, R.A. 1990: Analysis of wildlife radio-tracking data. - Academic Press, Inc., San Diego, California, USA, 383 pp.
- Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R. & Foster, M.S. 1996: Measuring and monitoring biological diversity. Standard methods for mammals. - Smithsonian Institution Press, Washington, D.C., USA, 409 pp.
- Wingfield, J.C. 2005: The concept of allostasis: Coping with a capricious environment. - *Journal of Mammalogy* 86: 248-254.
- Wood, S.N. 2006: Generalized Additive Models: An Introduction with R. - Chapman and Hall/CRC Press, Boca Raton, Florida, USA, 391 pp.