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

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Abstract

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* induces behavioural alterations. In particular, we expected that the roe deer would express 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, considering a period of 50 days after release. We compared the first ten days after release with the subsequent days for the following behavioural parameters: the 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 these 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 the most and fawns the 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 expressed 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 when behavioural alterations due to capture and handling may be pronounced.

Introduction

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 temperature, 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 the 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 sub-clinical 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), skinks *Oligosoma otagense* (Germano 2007) and bear *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 any 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 organism. 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, this study investigated whether the capture and handling of roe deer *Capreolus capreolus*, a medium sized ungulate, modifies 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.

Materials and methods

Study area

The study was carried out in a fragmented agricultural landscape of the Aurignac canton (N 43°13', E 0°52'), situated in the Comminges region of south-west 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, with agricultural crops on the increase. The human population is present 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, with about 21% of that 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 respectively about 34%, 33% and 7% of the total area (see Hewison et al. in press for more details).

The roe deer population is hunted on a regular basis by stalking during summer (June-August, bucks only) and by drive hunts with dogs during autumn-winter (September to 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 4-8 deer / 100 ha (Hewison et al. 2007).

Study population and data collection

From 2002-2008, roe deer were caught during winter (from 16th November to 27th 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 contention 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 less than 10 minutes). At the end of the capture event, all boxes were collected together 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 some information and to equip them with a collar. This phase lasted for approximately 10 minutes during which we recorded body weight, sex, hind foot length and we attributed an age class. Juveniles (less than one year-old) are distinguishable from older deer by the presence of a tri-cuspid third pre-molar milk tooth (Ratcliffe & Mayle 1992). For older deer, tooth wear was used to distinguish yearlings (18 months old) from adults of more than 2 years of age. Deer were then equipped with ear tags and a radio-collar with a twelve channel Lotek 3300 GPS (for home range and habitat use studies) and released on site. The total time from capture to release lasted several hours (from 115 to 416 min in 2009, not measured previously). Altogether, 112 roe deer were monitored (Table 1) and equipped with these 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, range = 1.7 - 2.3% for yearlings and range = 1.9 - 4.0% for fawns). Collars were programmed to obtain the localisation of the roe deer with a schedule of one GPS fix every 4 hours (first two winters) or every 6 hours (following winters). We performed differential correction in order to improve fix accuracy (Adrados et al. 2002) and 50% of fix locations were located within 14 m of their true position in our study area (Cargnelutti et al. 2007). All fixes (latitude, longitude) were converted to Lambert III coordinates using pathfinder Office version 2.7 (Trimble navigation Ltd, USA).

Statistical analysis

The ten capture sites were grouped into 3 landscape units based on contrasting landscape 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 03 May, 24 March and 09 April for the latest capture date of respectively adults, yearlings and fawns), 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, the animal may need several days before it exhibits “normal” ranging behaviour which we assumed to be similar to its behaviour prior to capture. We used generalized 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 (2 modalities), sex (2 modalities), landscape sector (3 modalities) and age class (3 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 ten 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 "several days or up to 1 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 (see Fig. 1a). We also performed the same model for each individual separately and looked for the point when the distance to the barycentre was equal to or less 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, likely disturbed by the capture event. 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, with the kernel method at 95%) in the model as a covariable to control for this effect. To test the statistical significance of these 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 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 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 (Benhaiem et al. 2008).

In terms of activity pattern, the GPS collar records movements of the collars with activity sensors (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, the HD sensor, computes the proportion of time that the head is in a downward position. These three measures are recorded every 5 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 is recorded as a percentage. We summed the activity values for the two different periods and we then reduced the number of activity variables by considering the first factorial axis of a principal component analysis (PCA) of these three variables (Dolédec & Chessel 1991). To compare 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 ($slope=0.86\pm0.04$). Regarding time after release (Fig 1a), there was a sharp decrease in the distance to the barycentre during the first 10 days, but then this levelled out at around zero metres, with no further discernible pattern ($F=90.52$, $edf=8.87$, $p<0.0001$). 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 (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 (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 (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 (P1=57.5±3.11% and P2=49.1±3.31%, t=4.62, df=111, p<.0001). Similarly, the mean distance to the nearest forest (DF) patch was significantly lower (DF1=50.9±5.66 m and DF2=63.6±6.68 m, t=3.10, df=111, p=0.0024) and the mean distance to the nearest source of human disturbance (DHD) was significantly higher (DHD1=343.2±20.75 m and DHD2=325.4±20.87 m, 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.

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 principal component analysis 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 compared to 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 levels. 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, while 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. Wahlstrom 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 fawn's mother was generally not caught in the same capture operation and hence the fawn's stress response was attenuated by the presence of his 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 if 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 re-establish 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 (to potential predators, disturbance, etc.) in open areas and are able to detect human presence farther away compared to closed habitats (Benhaiem 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 this species (Tufto et al. 1996). During winter, in more open cultivated areas, sheltered habitats (generally, 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 compared to random sites.

In our study, the stress of the capture process also induced a reduction in the overall level of activity of our roe deer. This type of effect has also been observed on captive red grouse (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, mallard 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, little data is available, but Blanc & Brelurut (1997) found a decrease of 40% in grazing activity of red deer hinds over a short period of 8 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 (Hewison 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 ten 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 with respect 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.

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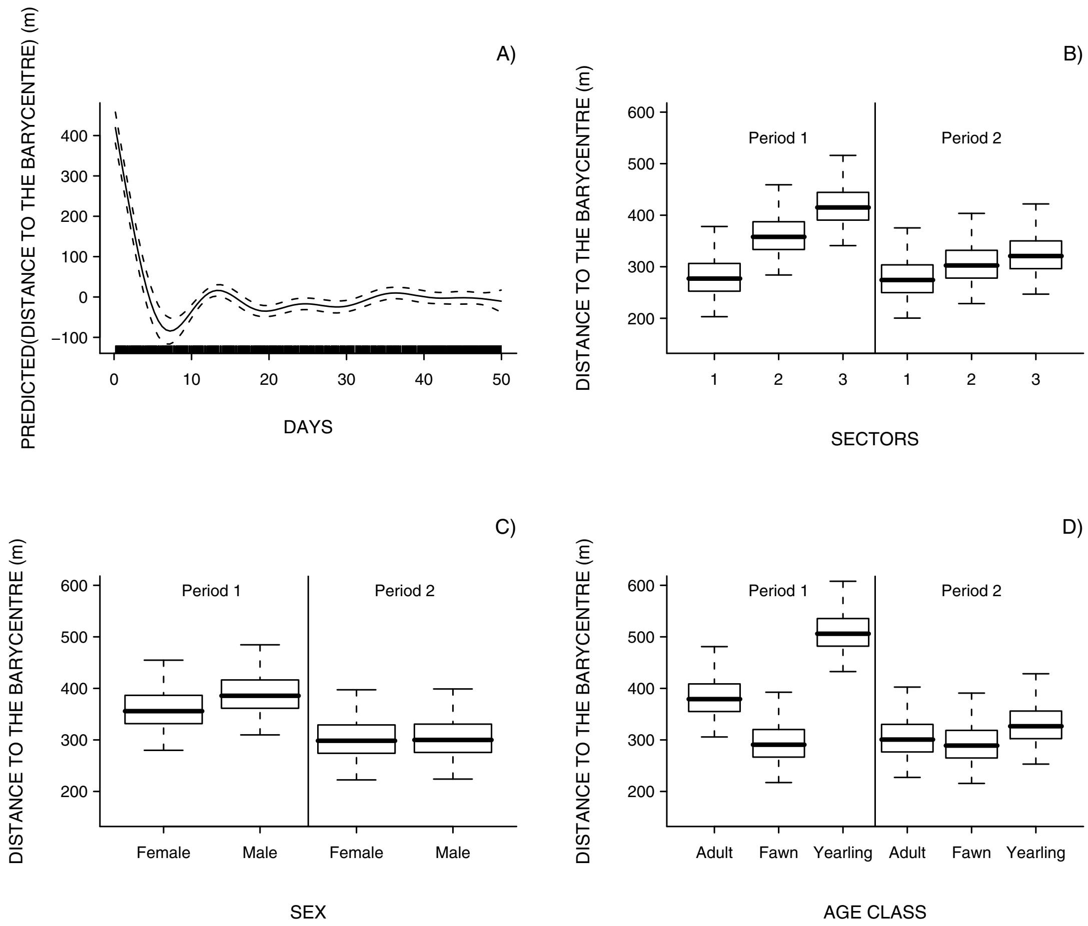
Table 1. The mean length of time (months) ±SE by year, sex and age class during which individual roe deer were monitored (with the sample size in brackets).

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

Fig. 1.Individual distances between GPS fixes and the barycentre of their fixes over the first 50 days predicted by the most-supported generalized additive mixed model for 112 roe deer (including the individual as a random effect): a) as a function of time after release, including a smoothing effect with a spline, b) the two-way interaction between period and sector of capture, c) the two-way interaction between period and sex and d) the two-way interaction between period and age class. 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.


A)
PREDICTED(DISTANCE TO THE BARYCENTRE) (m)
400
300
200
100
0
−100
0
10
20
30
40
50
DAYS
B)
DISTANCE TO THE BARYCENTRE (m)
600
500
400
300
200
Period 1
Period 2
1
2
3
1
2
3
SECTORS
C)
DISTANCE TO THE BARYCENTRE (m)
600
500
400
300
200
Period 1
Period 2
Female
Male
Female
Male
SEX
D)
DISTANCE TO THE BARYCENTRE (m)
600
500
400
300
200
Period 1
Period 2
Adult
Fawn
Yearling
Adult
Fawn
Yearling
AGE CLASS

581