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Reintroduction of roe deer *Capreolus capreolus* into a Mediterranean habitat: female mortality and dispersion

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During 1995-1997, 52 male and 52 female roe deer *Capreolus capreolus*, captured in the Forest of Trois-Fontaines in northeastern France, were introduced into the Petit Luberon state forest in southern France; of these 49 females (21 young that were < 1 year old and 28 adults that were > 1 year old) were monitored by radio-tracking. The overall mortality rate among the females monitored was 47% within one year of release. The first month following the release (February) was critical for the success of the operation as 35% of introduced animals died within this time span. It appears that stress was a major cause of mortality at this time, but traumatic deaths caused by drowning, collision with cars, and falling off cliffs were also frequent. The survival rate increased to 0.9 in spring, summer and early fall and decreased again during late fall and early winter. The high mortality rate occurring during this period may be explained by an increased mobility resulting from disturbance from wild boar *Sus scrofa* hunting. After the reintroduction, the animals stayed close to the release site (50% within 2.4 km, and 75% within 4 km), though the adults established themselves at longer distances than the young. The dispersion pattern of the females was not uniform throughout the study area: they preferentially settled down northwest of the release site, which may be explained by the topography of our study area and by the absence of human structures (roads, canals) in this area.

Key words: Capreolus capreolus, capture-recapture models, dispersion, Petit Luberon, reintroduction, roe deer, survival

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The roe deer *Capreolus capreolus* has been absent from the French Mediterranean region since the 18th century. Many authors attribute its disappearance to both the deforestation of the region at this time and the high hunting pressure it was subjected to (Cugnasse 1989, Cugnasse & Chiappin 1992, Maillard et al. 1999a). Although the roe deer was still absent from most Mediterranean areas in 1981 (O.N.C. 1985), two recent surveys have highlighted its progressive resettlement in the Mediterranean region during the last 10 years (Dubray et al. 1991, Gaudin et al. 1997). According to Cugnasse (1989) and to Cugnasse & Chiappin (1992), the recent recolonisation is mainly the result of numerous reintroductions, and was favoured by the expansion of the forest cover resulting from the decline in agricultural activity.

The recolonisation of Mediterranean habitats has seldom been studied at population scale. Biologists are increasingly concerned about the factors, whether demographic (survival and reproduction of reintroduced deer) or spatial (dispersion of released animals), determining the success of the settlement of roe deer populations (Maillard et al. 1999b). A good knowledge of these factors would be helpful in understanding the reasons for the large-scale development of roe deer in this kind of habitat. Moreover, the study of the settlement of roe deer populations after a reintroduction may be helpful in the field of conservation biology. For example, such data may help planning the reintroduction of the roe deer undertaken in Portugal (see Ferreira et al. 1996) to provide wolf *Canis lupus signatus* prey. More generally, data on common species like roe deer may help to plan the reintroduction of endangered ungulates.

This paper focuses on the factors affecting the dynamics of the settlement of a roe deer population, when 104 roe deer (52 males and 52 females) were reintroduced into a Mediterranean habitat, viz. the Petit Luberon State Forest, and among which only females were equipped with radio collars. We considered the development of the survival rate of introduced does in the year following the reintroduction, as well as possible effects of age and year of release on this rate. We also wanted to determine whether the animals tended to stay close to their release site, and whether the age of the does and their year of reintroduction affected the distance of dispersion.

Material and methods

Study area

The Petit Luberon state forest, which covers 3,300 ha, is situated in the southeast of the Vaucluse department, in southern France (Fig. 1). The topography of our study area is characterised by many steep cliffs and plateaus, with altitudes of 200-700 m a.s.l. Mean monthly temperatures ranged from 5°C in December-January to 23°C in July-August during 1995-1997, and mean annual rainfall in the area was of 776.7 mm (SE = 5.31), with an annual drought occurring in July-August.

The vegetation in the study area is characteristic of the thermo-Mediterranean stratum. There are five main vegetation types: dense scrubland of Kermes oak *Quercus coccifera* which represents the main woodland community (40%), pinewood of Allepo pine *Pinus halepensis* (20%) and coppice of Holm oak *Quercus ilex* (20%). Open scrublands, mainly made up of white-leaved rockrose *Cistus albidus*, common box *Buxus sempervirens* and prickly juniper *Juniperus oxycedrus*, represent 10% of the study area. The remaining 10% mainly consists of plantations and meadows. More than 1,200 herbaceous and shrub species have been registered in the Luberon (Guende 1993), and the management of the forest aims to preserve this biodiversity. The habitat thus remains open due to ground clearance operation conducted by the foresters, and to continuous grazing by flocks of sheep. Many canals and roads border the south and west sides of our study area. Local hunters indicated to us that the pre-reintroduction roe deer population was very scarce on the Luberon mountain, which was later confirmed by personal observation.

Capture

The reintroduced roe deer were captured in the Trois-Fontaines forest, in the Haute-Marne department in northern France (see Fig. 1). The area is managed by the 'Office national de la chasse et de la faune sauvage', mainly to produce animals to restock other forests (see a description of this area in Gaillard et al. 1993).

The roe deer were captured using linear drive nets (Van Laere & Boutin 1990). A capture area was defined for each capture session, and 2-m high stakes were stuck in the ground along all sides of this area except one (one stake every 5 m). The capture session occurred one week after this operation. Before the session, the nets were silently raised on the stakes by the 'catchers'. Then, the animals were driven toward the nets by local hunters accompanied by dogs, while the catchers stood in line close to the nets. When a deer ran into the net, the net

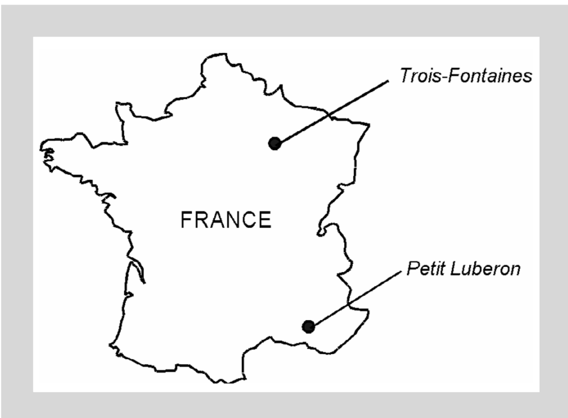

Figure 1. Location of the French state forests Petit Luberon and Trois-Fontaines.

unhooked from the supporting stakes, forming a pocket around the animal. Then, the nearest catchers quickly rushed to the deer to capture it. Each captured animal was sexed, weighed and aged according to its dentition pattern (Van Laere et al. 1989). In this paper, we will use the term 'young deer' for individuals < 12 months old, and 'adult deer' for individuals > 12 months old.

We captured 52 male and 52 female roe deer in January and February during 1995-1997. After their capture, the animals were shut up in an enclosure for a period of 2-10 days, during which they were fed with granules and fresh vegetables.

Transportation, reintroduction and monitoring of the released does

The captured roe deer were transported by truck from Trois-Fontaines to the Petit Luberon forest. On average, 15 roe deer were released during each introduction session (three sessions in February 1995, three sessions in February 1996 and one session in February 1997). The animals were all released from the same point. Among the released animals, 49 females were equipped with radio collars (10 adults and seven young in 1995, 13 adults and 12 young in 1996, five adults and two young in 1997). These does were located during the day, once or twice a week. The bearings were taken from a vehicle mounted with a Yaesu (290 RII) receiver linked to a directional seven-pronged Tonna antenna. We took three bearings for 70% of the relocations, and only two for the remaining 30%. The Lambert coordinates of the relocations were then computed using the Lenth maximum likelihood estimator (e.g. White & Garrott 1990), with the help of the locate II program (Nams 1990). The error ellipse covered < 1 ha for 92% of the relocations.

Monitoring of the reintroduced population

We monitored the development in population levels from 1996 to 2002 using the kilometric index (Vincent et al. 1991). Six circuits measuring 5-7 km were defined in our study area. For a given year, each circuit was travelled by foot eight times during February-March early in the day, and all the roe deer detected on the circuit were recorded. We thus computed a kilometric index (mean number of animals seen per kilometre) for each year during 1996-2002, following the methodology defined in Vincent et al. (1991). This index does not give a 'crude' estimation of the population size, but rather an index of the development in population levels when it is carried out each year under the same conditions (i.e. same observer, same circuits, same period; see Vincent et al. 1991). The kilometric index gave us an indication of the success of the reintroduction.

Data analyses

Survival of the reintroduced does

We estimated the survival of the introduced roe deer during the first year after the reintroduction. Each year of reintroduction was divided into seven periods: 1) February (the month of release), 2) March-April, 3) May-June, 4) July-August, 5) September-October, 6) November-December and 7) January-February. We assessed the survival of the roe deer during each of these periods using the capture-recapture models developed by Lebreton et al. (1992). We thus constructed a capture-history matrix, with 49 rows and seven columns. At the intersection of the i^{th} row and of the j^{th} column, 1 indicated that the i^{th} animal was alive at the beginning of the j^{th} period, and 0 indicated that it was dead (or that its transmitter had failed). We then built several models for the survival rate (Table 1), allowing for the

Table 1. Modelling of the survival rate of 49 reintroduced does in the Petit Luberon Forest, according to age (A: young < 12 months old, adult > 12 months old), year of reintroduction (Y: 1995, 1996 and 1997), period of the year (T: February, March-April, May-June, July-August, September-October, November-December, January-February), and all interactions between the three factors (indicated by a dot). AIC_c is the Akaike Information Criterion corrected for small samples ($\Delta_i = AIC_c$ - [minimum AIC_c]), N is the number of estimated parameters, and w_i are the Akaike Weights[1].

	Model	Deviance	N	AIC_c	Δ_i	w_i
1	A+Y+T+A.Y+A.T+Y.T+A.Y.T	111.67	42	218.68	52.37	0.00
2	A+Y+T+A.Y+A.T+Y.T	121.45	31	195.26	28.94	0.00
3	A+Y+T+A.T+Y.T	125.45	29	193.69	27.37	0.00
4	A+Y+T+Y.T	134.93	21	182.12	15.81	0.00
5	Y+T+Y.T	134.93	20	179.63	13.31	0.00
6	A+Y+T+A.T	137.21	16	172.18	5.87	0.03
7	A+T+A.T	138.92	14	169.20	2.88	0.12
8	A+Y+T	147.55	11	170.95	4.64	0.05
9	Y+T	147.55	10	168.72	2.40	0.15
10	A+T	149.53	9	168.48	2.16	0.17
11	*T*	*149.56*	*8*	*166.31*	*0.00*	*0.49*
12	Null	175.87	2	179.93	13.61	0.00

[1] The w_i may be interpreted as the probability that the model i is the actual best model among those in competition. These weights may be summed over several models to assess the importance of a variable (e.g. for the Age, w_i = 0.17 + 0.05 + 0.12 + 0.03 = 0.37).

main effects of the period, the age of the animal (adult or young) and the year of reintroduction (1995, 1996 and 1997) as well as all interactions between these factors. The probability of recapture was considered constant for all classes of animals. We used the Akaike Information Criterion corrected for small samples (AIC_c) to select the more parsimonious model, according to the recommendations of Burnham & Anderson (1998). We also computed the Akaike weights (w_i) using the formula:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_r)},$$

where Δ_i is the AIC_c for model i minus the minimum AIC_c. The weight w_i may be interpreted as the probability that the model i is the actual best parsimonious model among the R models in competition. A measure of the importance of each variable (age, year or time period) is to sum the Akaike weights over the subset of models that include this variable (Burnham & Anderson 1998). These analyses were performed using the SURGE program.

Dispersion of the reintroduced animals

We computed the distance of dispersion as the distance between the release site and the arithmetic mean of the coordinates of the animal's relocations. After their release, a few monitored deer showed a period of spatial instability, during which they were exploring their new habitat (Sempéré et al., Maillard et al. 1999b). However, all animals seemed to have established a stable home range three months after their introduction into the area. We therefore used all relocations collected at least three months after the release of the animals for the computation of the distance of dispersion.

We used a Generalised Linear Model (Aitkin et al. 1989) to test the effects of age (young or adult) and year of release (1995, 1996 or 1997) as well as interactions between these factors on the log-transformed distance of dispersion of the released animals. We used a backward procedure to account for the unbalanced design, testing first the interactions and then the main effects of factors (Aitkin et al. 1989). We analysed the pattern of dispersion of the deer throughout the study area using similar analyses: we wanted to determine whether the animals settled down randomly over the study area. We thus divided the study area into four 'quarters': (i) northeast, (ii) northwest, (iii) southwest and (iv) southeast of the release site. We then modelled the number of deer in each 'quarter' according to its orientation (using a log link). This allowed us to compare the dispersion pattern of introduced deer to a random spatial distribution. Finally, we tested an effect of the distance of dispersion on the mortality rate within one-year timespans, using a generalised linear model (with a logit link). All these analyses were carried out using the GLIM software (Francis et al. 1993).

Results

Survival rate of reintroduced deer

The observed survival rate of the does monitored in our study was very low. In fact, only 53% of the does (26 animals) were still alive one year after the reintroduction. The best parsimonious model of the survival rate was the Cormack-Jolly-Seber model (Lebreton et al. 1992), i.e. the model estimating the survival rate only according to the time period (see Table 1). There was indeed a considerable time variation in the survival rate of the released does ($w_i \approx 1$ for this factor). The first month following the reintroduction (February) was a critical period for the animals, the observed mortality rate being very high (Fig. 2). Half of the deaths that occurred during this period were traumatic (collision with cars: 2 animals; drowning: 1 animal; falling off cliffs: 3 animals), and the other half were unexplained (six animals). It is likely that stress in some form (e.g. post-capture myopathy) accounted for a large proportion of these losses, because many unexplained deaths occurred a few days after release. The survival rate was higher during spring and summer ($\Phi \approx 0.9$ for each 2-month period; see Fig. 2). During this period, the causes of death were traumatic in 63% of the cases (drowning: 2 animals; falling

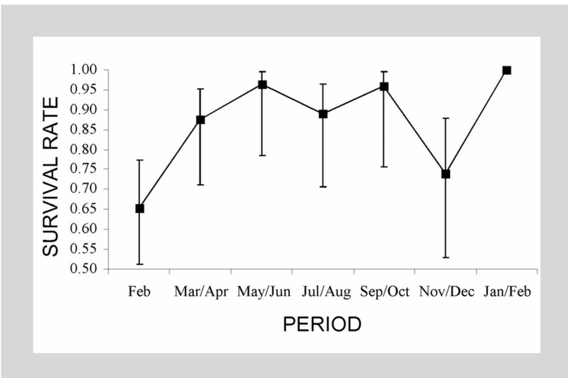

Figure 2. Development in the survival rate of the female roe deer introduced in the Petit Luberon forest, according to the Cormack-Jolly-Seber model selected in Table 1.

Table 2. Mortality rate over one year of 49 female roe deer monitored in the Petit Luberon state forest. Adult females are > 12 months old, young females are < 12 months old.

Year of release	Age	Number of dead animals	Mortality rate (%)
1995	Adult	4 out of 10	40.0
	Young	6 out of 7	85.7
1996	Adult	4 out of 13	30.7
	Young	4 out of 12	33.3
1997	Adult	3 out of 5	60.0
	Young	2 out of 2	100.0
All years	Adult	11 out of 28	39.3
	Young	12 out of 21	57.1

off cliffs: 2 animals; poaching: 1 animal), and unknown for three animals. Finally, the survival decreased again during late fall and early winter. The deaths that occurred during this period were solely traumatic (drowning: 1 animal; hunting: 1 animal; collisions with cars: 2 animals).

The effects of age ($w_i = 0.35$) and year of reintroduction ($w_i = 0.37$) on the survival rate of the does were far less important than the effect of time period. However, even though they do not appear in the best parsimonious model, these effects were present: the mortality rate was higher in 1995 and 1997 than in 1996 for all age classes (Table 2), and young deer died more frequently within the one year time span than adults, irrespective of their year of reintroduction.

Dispersion of the introduced animals

Most of the animals stayed close to their release site. Half of the monitored animals settled down within 2.4 km, and 75% within 4 km of the release site. The largest distance of dispersion was covered by an adult female, which settled down 20 km from its release site (Fig. 3). We found that age had a significant effect on distance of dispersion of the deer ($F_{1,29} = 8.39$, $P = 0.007$). Adult females established themselves at longer distances from the release site ($\bar{x} = 4.5$ km, SE = 1.1) than young deer ($\bar{x} = 1.5$ km, SE = 0.3; see Fig. 2). On the other hand, neither the year of reintroduction ($F_{2,27} = 0.73$, $P = 0.49$) nor the interactions between year and age ($F_{2,25} = 1.24$, $P = 0.31$) affected the distance of dispersion of the animals.

The dispersion of the animals throughout the study area was not uniform (Fig. 4). The does settled down preferentially northwest of their release site ($\chi^2_3 = 12.72$, $P = 0.005$). There was no significant difference between the three other 'quarters' (northeast, southwest and southeast: $\chi^2_2 = 2.67$, $P = 0.26$). Moreover, we found no relationships between the distance of dispersion of the does and their mortality rate ($\chi^2_1 = 0.006$, $P = 0.94$).

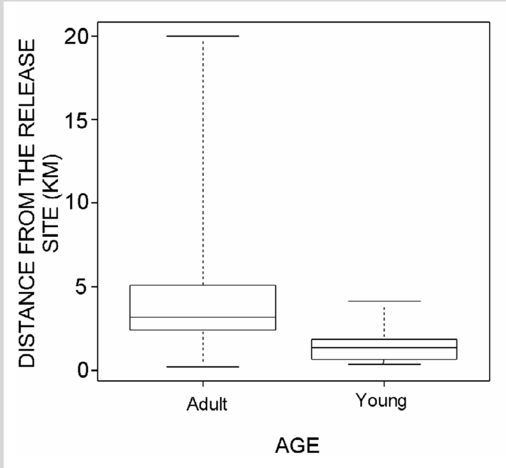

Figure 3. Boxplot of the distance of dispersion (in km) of the introduced female roe deer according to their age (adults: > 12 months old; young: < 12 months old).

Monitoring of the reintroduced population

While the population level was rather low before 1995, it increased considerably after the reintroduction and especially after 1997 (Fig. 5). Thus, despite the high mortality rate occurring in our study, the reintroduction allowed the rapid development of a roe deer population in the Petit Luberon forest. This operation can therefore be considered as successful.

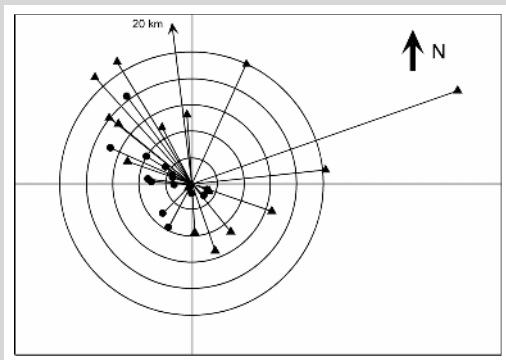

Figure 4. Spatial pattern of dispersion of the monitored roe deer from their release site in the Petit Luberon state forest (1 circle = 1 km). Data are presented for adult (>12 months old; ▲) and the young females (<12 months old; ●), and the division of the study area into four quarters is indicated. One adult female moved 20 km from the release site in a northerly direction before settling down.

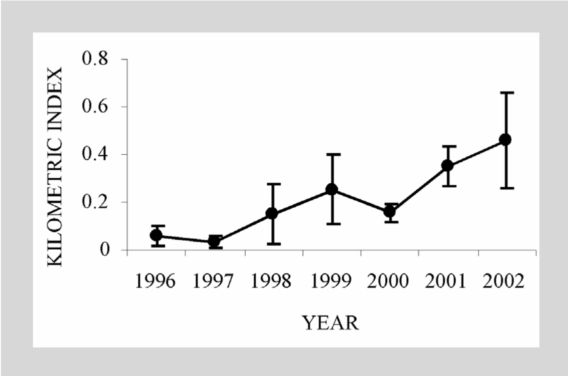

Figure 5. Estimations of the Kilometric Index from 1996 to 2002 in the Petit Luberon state forest (± SE).

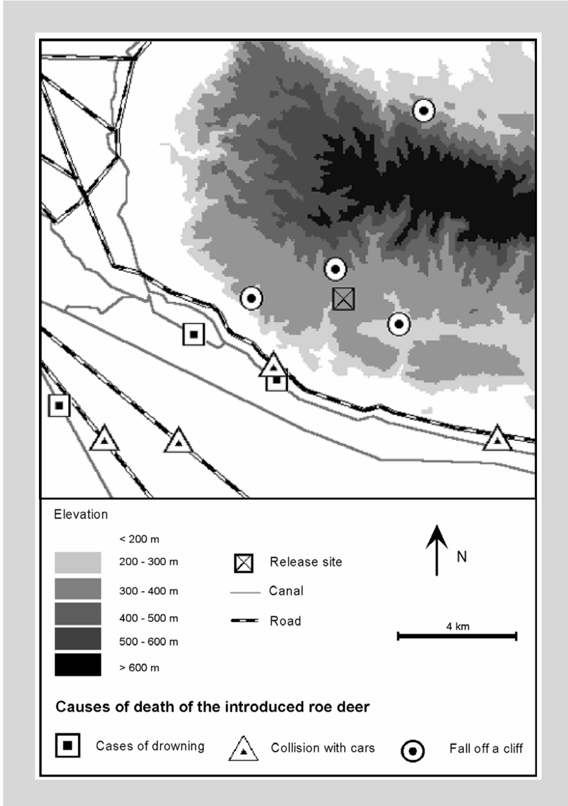

Figure 6. The Petit Luberon state forest with indications of elevation and locations of roads and canals. Locations of traumatic deaths with known causes are indicated.

Discussion

Mortality

The mortality rate that was recorded in our study was quite high in comparison to other studies on introduction of roe deer in Mediterranean or temperate habitats, but it was lower than those reported from mountain habitats (Table 3). The mortality, being essentially traumatic, should be ascribed to the particular structure of our study area and to the release conditions, rather than to the Mediterranean climate or vegetation. The numerous cliffs encountered in the Petit Luberon forest represented a danger for the deer, since falling off cliffs was the prevalent cause of death. Further, the presence of human infrastructure affected survival; collisions with cars and cases of drowning, which were also frequent, occurred only south and west of the release site, where several roads and canals were encountered (Fig. 6). Because of the steep banks of these canals, the roe deer could not cross them easily, and this has already been reported as a cause of deer mortality (CEMAGREF 1982). The infrastructure was close to the release site, and this may explain why we could not highlight any negative effect of the distance of dispersion on the survival of the does.

The first month following the reintroduction was critical for the success of the operation and many animals died during this period. Stress seems to have led to the death of numerous animals, though it was not directly measured. Indeed, this factor appears to be a prevalent cause of mortality in the literature dealing with species reintroduction (Dubray et al. 1990, Lecomte 1990, Ferreira et al. 1996, Rosell et al. 1996). After their capture in the Trois-Fontaines forest, the does were penned up in an enclosure for a period of 2-10 days, which may have increased their stress. Further, some of them had been equipped with radio collars at their re-

Table 3. Comparison of the annual mortality rate of introduced roe deer in Mediterranean areas, in temperate forests and in mountain forests. N gives the number of animals released.

Country	Habitat type	N	Mortality (%)	References
France	Mediterranean garrigue	49	47	Our study
France	Mediterranean garrigue	13	15	Bideau et al. 1990
Spain	Mediterranean garrigue	20	5	Rosell et al. 1996
France	Supra-Mediterranean garrigue	13	15	Maillard et al. 1999b
France	Temperate forest of L'étoile	41	7	Sempéré et al. 1986
France	Temperate forest of Absie	14	0	Sempéré et al. 1986
Italy	Mountain forest of Cueno	7	87	J-C. Gaudin, unpubl. data
France	Mountain forest of Uvernet-Fours	12	83	Y. Léonard, unpubl. data

lease site, requiring additional manipulation before their release. It seems likely that if the animals had been equipped with collars on the capture site and immediately translocated from the Trois-Fontaines forest to the Petit Luberon forest, the mortality rate would have been reduced. Unfortunately, little information has been collected on the handling and treatment of animals before their release, and it was not possible to explicitly test the effect of handling on doe survival.

Although the survival rate of the does increased in spring, summer and early fall, it was still rather low: the estimated survival rate was 0.9 for two months during this period, whereas the same value has been estimated in Trois-Fontaines for a whole year (Gaillard et al. 1993). Likewise, the high observed mortality was essentially due to the particular structure of our study area (topography and human structure).

There was a considerable decrease in doe survival during late fall and early winter. The increased mortality during this period may have been due to increased mobility of the animals in response to disturbance caused by wild boar *Sus scrofa* hunting. This factor has already been reported to be a cause of disturbance for the roe deer (Gaudin 1991). Wild boar hunting is a group sport involving pursuit with packs of long-legged hounds, and is practised during this period. In our study area where the roe deer is scarce, the dogs are not trained to search only for wild boars, and they flush and chase deer as well as boars (J-C. Gaudin, pers. obs.). The resulting high mobility lead to an increased risk of death (collisions with cars, falling off cliffs; see Jeppesen 1984).

Several authors have highlighted an effect of age on roe deer survival in native populations, the mortality being higher among the young than among adults (e.g. Gaillard et al. 1993). Indeed, the survival of the fawns is generally weaker during their first summer of life (early survival; Gaillard et al. 1997) and during their first winter of life (Gaillard et al. 1992). In our study, the mortality was slightly higher among young deer than among adults, but this difference was negligible in comparison to the time-period effect. The does were released in February, by which time the two critical periods in fawn survival had elapsed. The survival of young was therefore similar to the survival of adults, which may explain why the age effect does not appear in the best parsimonious model.

Finally, the release conditions varied between years (experience of the manipulators, site of fitting with radio collars, time spent in the enclosure), leading to variable stress conditions, which may explain the between-year differences in mortality rate, though they were rather small.

Dispersion

Most female deer settled down in the vicinity of their release site, even though adults tended to disperse further than the young. The mean distances of dispersion observed in the Petit Luberon were similar to the mean distances computed in other studies for both adult and young females, both in Mediterranean areas (Ferreira et al. 1996, Rosell et al. 1996, Maillard et al. 1999b) and in more temperate habitats (Sempéré et al. 1986). However, the pattern of dispersion was not uniform throughout the study area: the settlement of roe deer was more frequent northwest of the release site. Although in most studies the dispersion of introduced deer throughout the study area was uniform (Sempéré et al. 1986, Dubray et al. 1990), several authors pointed out that certain habitat characteristics, such as roads and canals (Bideau et al. 1990, Rosell et al. 1996), or topography (Maillard et al. 1999b) may limit the dispersion of the individuals in certain directions. The presence of roads and canals south of the study area may indeed have prevented the deer from dispersing in this direction, which would explain the apparent avoidance of this part of the study area.

The topography of our study area may also have affected the dispersion: it is likely that the Régalon gorges and the Galère valley, two very steep valleys southwest of the release site, have limited dispersion in this direction. However, the avoidance of the northeastern part of the study area is somewhat difficult to explain, since there was no 'natural barrier' to dispersion in this direction. Only three female deer settled down in this direction, and they established themselves at a long distance from the release site (see Fig. 3). Numerous factors may be involved in the determination of the space occupancy of the roe deer, such as the structure of the vegetation (e.g. Blant 1987), the location of water sources (Danilkin & Hewison 1996) or human disturbances (Vincent et al. 1998). However, we could not identify any differences between these factors between the northeastern part and the rest of the study area. It therefore seems difficult to explain the apparent avoidance of this part of our study area.

Management implications

The success of a species reintroduction is dependent on several factors. Some are linked to the area of reintroduction and are impossible to overcome. Thus, the topography of the study area and the presence of human structures may greatly affect both the survival and the dispersion of introduced roe deer. Therefore, biologists should reduce all controllable sources of mortality when planning reintroductions, and especially the sources of stress. The time elapsed between the capture of animals and their release should be kept as short as possible (Gauthier & Villaret 1990), and the sources of stress should be minimised during the transportation of animals (Lecomte 1990). The handling of animals should be kept at a minimum, and should be carried out by experienced field workers. The age of reintroduced animals may also be important. In the case of the roe deer, biologists should reintroduce young animals rather than adults, because they tend to settle down closer to the release site than adults, which increases the probability of population establishment. The period of reintroduction should be chosen according to the biology of the species. It is indeed important that the reintroduction of a species is planned at the time when a maximum of the reintroduced animals will survive. Thus, February seems to be the best month for roe deer reintroductions, since the summer and winter mortality of fawns have already occurred and since human disturbances are scarce at this time (no hunting, no mushroom gathering, no sheep grazing). Finally, monitoring the development of the population will allow the success of the reintroduction to be assessed (Bigan 1990). We stress that a biological indicator, like the kilometric index for the roe deer, may give a good indication of this success with a low cost (Vincent et al. 1991).

Despite the high mortality rate that occurred in our study, this reintroduction has been a success. Most reintroduced females settled down close to the release site, which has allowed the rapid development of a population on the Luberon mountain. Although we lack data on males, this study confirms that roe deer from northern France may easily adapt to the Mediterranean habitat.

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