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Demographic crash associated with high parasite load in an experimental roe deer (*Capreolus capreolus*) population

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Abstract In March 2002, ten roe deer (*Capreolus capreolus*) were released in a partly wooded 14.2-ha enclosure to investigate the effect of high population density on vegetation cover and demographic parameters. However, in mid 2003, five animals died after rapid emaciation. Two other deer were killed to carry out further post-mortem examination. In addition to a general loss of body mass, and injuries in males caused by the healthiest of them, we found a high level of parasitism. The remaining animals received anti-parasite treatment, and four other treated roe deer were added into the enclosure. All the deer were then captured and treated against parasites twice a year, the fawns being removed when first captured. Four years after the crash, the population seemed healthy: deaths no longer occurred; mean adult body mass reached 27.6 kg in March; females produced on average 1.6 fawns per year, with a mean body mass of 13.8 kg in October, and 16.7 kg in March. Furthermore, undergrowth cover changed little since March 2004. These results suggest that outbreaks of parasites may cause population crashes in high-density situations before the onset of nutritive stress, and may explain certain cases of ‘abnormal’ (massive) mortality recorded in roe deer.

Key words Parasite outbreak – mortality – body mass – food resources – social stress

Introduction

The roe deer (*Capreolus capreolus*) is currently abundant in Western Europe. Having almost become extinct in parts of southern Europe because of habitat loss and over-hunting in the first half of the last century, its numbers started increasing 20-40 years ago (Lovari *et al.* 2008), and are still increasing, as shown by the yearly numbers of animals hunted (Saint Andrieux and Pfaff 2007) and of collisions with cars (Mouron *et al.* 1998). High deer densities impacting on vegetation (Maizeret *et al.* 1989; Rooney and Dress 1997; Augustine and McNaughton 1998), population growth is expected to progressively decline because of food depletion. This assumption is supported by studies providing evidence for ‘density-dependence’ of some demographic parameters in several deer species (Mysterud *et al.* 2001; Solberg *et al.* 2001; Stewart *et al.* 2005). In high-density roe deer populations, the adult females’ fecundity, and the fawns’ body mass and survival are reduced (Vincent *et al.* 1995; Gaillard *et al.* 1996, 1997; Andersen and Linnell 1998), and the age at first breeding is delayed (Gaillard *et al.* 1992).

However, changes in population size are not always progressive, and roe deer populations are sometimes subjected to sudden, massive mortality, whose causes remain unclear (Lamarque *et al.* 1999).

We carried out an experiment to investigate the effect of high roe deer density on woodland vegetation and on the population’s demographic parameters.

However, an unexpected population crash occurred *ca.* one year after the start of the experiment, leading us to search for its causes, and stop the trend. We report the results obtained in the present paper because they may shed light on the cases of massive mortality sometimes occurring in natural roe deer populations.

Materials and Methods

The study was conducted in a 14.2-ha enclosure in the INRA (National Agronomy Research Institute) experimental station of Gardouch, situated in South-West France (43°22’N 1°40’E). It includes an 8.9-ha area of woodland, and two fallows of 3.9 and 1.4 ha, which were cut twice a year to allow observation from towers. The sylviculturally important and commonest tree in the woodland was the pubescent oak (*Quercus pubescens*). The other main trees and shrubs were the field maple (*Acer campestre*), wild service-tree (*Sorbus torminalis*), common hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), dog rose (*Rosa canina*), dogwood (*Cornus sanguinea*), and wayfaring tree

(*Viburnum lantana*). The undergrowth consisted mainly of ivy (*Hedera helix*), brambles (*Rubus* sp.), privet (*Ligustrum vulgare*), knee holly (*Ruscus aculeatus*), and secondarily of wild madder (*Rubia peregrina*), spurge laurel (*Daphne laureola*), and honeysuckle (*Lonicera periclymenum*).

In March 2002, ten wild roe deer (five males, and five females, all two–four years old with the exception of a yearling female) were captured in the military area of ETBS (Establishment of Technical Experimentation) near Bourges (France) then released in the enclosure. However, dogs that entered the enclosure in autumn 2002 killed one of the males, and above all, a population crash occurred in mid 2003. Accordingly, the population was supplemented in November 2003 with four roe deer (two adult females originating from an enclosure of the Chizé reserve (France), and two male fawns born in small enclosures of our experimental station).

From March 2003, captures were carried out twice a year, in March and October, in order to weigh the deer using an electronic balance, and remove the young of the year from the enclosure. The young that escaped capture in October when 4–5 months old, were invariably captured the following March. After the population crash, all the deer of the enclosure received an anthelmintic treatment (ivomec-D®) on each capture. On the population crash, we estimated the parasitic load, searching for external and internal parasites on dead animals: fresh faecal samples collected from dead animals or on the ground were examined by the MacMaster (Raynaud 1970) and the Baermann (Cabaret *et al.* 1980) methods, to estimate the number of eggs/larvae per gram. Gastrointestinal parasites were identified after egg incubation and larval growth. After the crash, we collected fresh faeces from every captured animal and estimated the parasite load (number of eggs/g).

Throughout the study, woodland vegetation was surveyed each year in February, using the Aldous method (Aldous 1944): cover and browsing intensity were assessed for each ligneous species 0–120 cm above ground in 36 circular plots of 40 m² each, located at the nodes of a 50-m grid established on a map of the wood. We did not consider herbaceous species cover, which is too dependent on immediate weather conditions in February. Browsing intensity was only assessed to determine which species were regularly consumed by roe deer and which were not. In each plot, the cover of each species was estimated using five classes: absent (class 1), ≤ 5% (class 2), 6–20% (class 3), 21–50% (class 4) and > 50% (class 5). We then used the median value of each class (0, 2.5, 12.5, 35, and 75%) to calculate cumulated cover for each plot, as the sum of individual species' cover. Three sets of plants were considered: (1) the 26 ligneous species present in the woodland, to provide an estimate of the overall cover; (2) the three species that were both consumed by roe deer and still leafed in late winter, i.e. brambles, ivy, and privet (referred to as 'food species'), to provide an index of food availability; (3) three species that were also leafed in late winter but not consumed by roe deer, i.e. knee holly, wild madder, and spurge laurel (referred to as 'non-food species'), to allow the evolutions of food and non-food species to be compared. Note that the cumulated cover ranged between 0 and a maximum value = 75% x number of species taken into account. The yearly variations of cumulated cover were analysed using a linear mixed effect model with year as fixed-effect factor, and plot as random-effect factor. Analyses were made on log-transformed data in order to homogenise variance. The model was fitted in R, using the lme function (R Development Core Team 2005). In the Results section, data are presented as untransformed means ± SE.

Results

In spring 2002, i.e. two–three months after the population foundation, the four females more than one year old gave birth to 1.8 ± 0.3 fawns. In March 2003, the body mass of these young was 13.4 ± 0.9 kg. Compared to March 2002, the body mass of the yearling female showed a 6.1-kg increase, while that of the other females showed an increase of 1.4 ± 0.4 kg; the body mass of males was stable except for one, which lost 4.8 kg (Fig. 1).

Fig. 1: Body mass of the enclosure's roe deer (dotted lines: the three animals that survived the crash, solid lines: other animals; black diamonds: males; white diamonds: females). Single points correspond to fawns native to the enclosure and removed on their first capture (in October or following March).

However, two females died after rapid emaciation in May and July 2003, and three males were found killed by the fourth male in May 2003. A third emaciated female and the remaining male were captured on mid-July and killed to carry out additional post-mortem examination. In addition to injuries in the three males found dead, we found a

general loss of body mass (-3.6 ± 0.6 kg since March; Fig. 1), and a high level of parasitism. Animals showed tick (*Ixodes ricinus*) and louse infestation (mallophaga), associated with alopecia, and internal parasitism. We recorded many œstid larvae (*Cephenemya* sp.) in the sinuses and the trachea ($n = 41.6 \pm 11.3$), a mean of 550.0 ± 118.4 eggs/g in the faeces, and identified gastrointestinal (*Trichostrongylus* sp., *Spiculoptera* sp., *Ostertagia* sp., *Chabertia-Oesophagostomum* sp. and *Trichuris* sp.), and lung parasites (*Dictyocaulus* sp.). On the other hand, the analyses did not reveal any pestivirus or paratuberculosis (*Mycobacterium paratuberculosis*).

The last two adult females (which had lost 2.0 and 2.8 kg since March, respectively) and a male fawn were caught in August 2003, and received the anthelmintic treatment in an attempt to reverse the disastrous trend. They all showed an increase in body mass when captured in autumn 2003 (Fig. 1). In contrast, a female fawn that was not caught in summer weighed only 8.6 kg in autumn. Killed for autopsy, she showed external and internal parasitism (700 eggs/g), was affected by a contagious ecthyma, a nephritis, and was dehydrated.

The four roe deer added into the enclosure in November 2003 raised the population to seven animals (four adult females, and three young males). Without any supplementary food but receiving the anthelmintic treatment twice a year, these seven individuals exhibited a relatively high body mass in March 2005, 2006 and 2007 (mean: 26.8 ± 0.5 kg; Fig. 1). All the females gave birth in 2005, 2006 and 2007, with an average of 1.6 ± 0.2 fawns per female; the body mass of young was 12.8 ± 0.8 kg in October (2004 to 2007) and 16.7 ± 1 kg in March (2005 to 2007). Parasitic charge remained almost null in adults (7.8 ± 3.4 eggs/g), and acceptable in the young, never treated, animals when first captured (138.5 ± 33.1 eggs/g).

Fig. 2 Cumulative cover, between 0 and 120 cm above ground, of the 26 ligneous species of the woodland (black line), of the three main ligneous species leafed in late winter and consumed by roe deer (brambles, ivy and privet: dark grey line), and of three ligneous species leafed in late winter but not consumed (knee holly, spurge laurel and wild madder: light grey line). Bars are the SE for the 36 sampling plots used throughout the experiment.

Cover of under-storey vegetation declined between February 2002 and February 2004 (Fig. 2): in 2004, the cumulated cover of all the ligneous species was 61.4% that in 2002, while the cumulated cover of the three main food species was 47.8% that in 2002. The decrease was significant for the 'food species' ($F_{1,71} = 76.34$; $p < 0.0001$), and for all the ligneous species ($F_{1,71} = 74.09$; $p < 0.0001$), since the main species consumed by roe deer were also the most abundant in the undergrowth. Within the same interval, the cover of the 'non-food species' did not vary ($F_{1,71} = 0.01$; $p = 0.92$). From February 2004, the cover of the 'food species', and of all the ligneous species remained stable ($F_{1,107} = 0.42$; $p = 0.52$, and $F_{1,107} = 0.08$; $p = 0.78$, respectively), while that of the 'non-food species' increased slightly ($F_{1,107} = 10.46$; $p < 0.002$).

Discussion

Population density in our enclosure (70.4 adults / km² at the start of the study, 49.3 from autumn 2003) was high in comparison with figures published for natural roe deer populations, where density estimates rarely exceed 30 deer / km² (Vincent *et al.* 1995; Gaillard *et al.* 1997; Kjellander *et al.* 2006, but see Gill *et al.* 1996). However, roe deer populations have high growth potential, and are mostly underestimated (Andersen and Linnell 2000).

In our high-density situation, browsing rapidly led to a decline in the under-storey vegetation, mainly depleting the abundance of food plants available in late winter. However, this trend stabilized from two years after the start of the study. On the other hand, one year after the deer introduction, five out of nine animals died after rapid emaciation. The final cause of death was harsh fights in males, but remained unclear in females. It is very unlikely that the deer became weak from starvation. All died or were dying between May and August, *i.e.* during the most productive period of the year. According to Aguirre *et al.* (1999), mortality due to starvation occurs during late winter and early spring. Moreover, no deer died or lost weight after September 2003, despite the ongoing decrease of food plant availability until late winter 2004. Actually, the body mass of roe deer remained high during successive winters, that of the young being 62.4% that of adults in March, which is considered as characteristic of highly productive populations (Gaillard *et al.* 1997).

The immediate stop of emaciation and mortality after anthelmintic treatment strongly supports the hypothesis of parasitic outburst as the final cause of death in females. This could be explained by the high roe deer population

density: gastrointestinal nematodes are abundant in wild ruminants and their transmission rates depend on host population density (Drozdz and Dudzinski 1993; Arneberg 2001). Heavy infections may impair body condition (Zaffaroni *et al.* 1997), survival (Gulland 1992; Milner *et al.* 1999) or productivity (Fox 1997; Stien *et al.* 2002), reducing the immune reactivity of animals (Gasbarre (1997). Ectoparasites such as ticks or louses are also part of the normal fauna of mammals, and may impair body condition in high-density situations (De Bosschere *et al.* 2006). Furthermore, we suspect that the high-density situation acted as a source of chronic social stress, depleting immunoresistance and the physical condition of the animals, as shown to occur in many mammalian species (rats: Dhabhar and McEwen 1997; prairie voles: Sinclair and Lochmiller 2000; swine and cattle: Salak-Johnson and McGlone 2007; human beings: Segerstrom and Miller 2004).

In natural conditions with low hunting pressure, roe deer population densities may progressively increase and the impact on vegetation will become accentuated year by year. In these conditions, the number of fawns per adult female, juvenile body mass and consecutively adult body mass should decrease, this density dependence being more pronounced in low quality habitats (Pettorelli *et al.* 2002; Kjellander *et al.* 2006; Toigo *et al.* 2006). Nevertheless, our results suggest that an often overlooked mortality factor related to high density could be outbreaks of parasites or other diseases. Focardi *et al.* (2002) reported a population decline due to an enteropathogenic strain of *Escherichia coli*. In our study, the population crash occurred before the emergence of a food-limiting factor, probably because the high density was reached suddenly. High density led to (i) a rapid transfer of parasites between animals, and (ii) a high degree of social stress, which plausibly contributed to immunodepression.

These results shed some light on the problem of massive mortality found in several roe deer populations, sometimes before the emergence of a gap between the population density and the food availability in its habitat. Massive mortality preferentially affects high-density populations, and parasitic load seems higher in animals in the high-mortality context than in controls. It would be useful to carry out standardised faecal egg counts and autopsies in healthy populations and in populations showing 'abnormal' mortality, to calibrate a scale of infestation in relation to the body condition of the animals and to estimators of population density.

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