Hind Foot Length: An Indicator for Monitoring Roe Deer Populations at a Landscape Scale

AUDREY ZANNÈSE, Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, Castanet-Tolosan Cedex, 31326, France

ALAIN BAÏSSE, Fédération Départementale des Chasseurs du Tarn, Albi Cedex, France

JEAN-MICHEL GAILLARD, Unité Mixte de Recherche N° 5558 'Biométrie et Biologie Evolutive', 69622 Villeurbanne Cedex, France

A. J. MARK HEWISON, Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, Castanet-Tolosan Cedex, 31326, France

KARINE SAINT-HILAIRE, Fédération Régionale des Chasseurs Midi Pyrénées, Toulouse Cédex 5, France

CAROLE TOÏGO, Office National de la Chasse et de la Faune Sauvage - CNERA Cervidés-sanglier, 38610 Gieres, France

GUY VAN LAERE, Office National de la Chasse et de la Faune Sauvage - CNERA Cervidés-sanglier, 79360 Villiers-en-Bois, France

NICOLAS MORELLET,¹ Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, Castanet-Tolosan Cedex, 31326, France

Abstract

Wildlife managers frequently use estimates of population densities to guide ungulate management. Because it is nearly impossible to obtain accurate counts, these estimates are based on indices. Thus, managers continue to seek new index methods that could help them better monitor and manage ungulate populations. In this paper we examine the usefulness of hind foot length as an ecological indicator of density dependence for monitoring roe deer (Capreolus capreolus) populations. We used the hind feet of all roe deer shot over an entire province for 13 years that were collected by wildlife managers from the Tarn Hunter Federation (France) to conduct this research. Information on the sex, date, and shooting locality were recorded by hunters, and animal age was determined by wildlife managers. We divided the province into 3 biogeographical regions and investigated the relationship between hind foot length of roe deer fawns, spring and summer climate (temperature and precipitation), and an index of deer density (number of shot roe deer per square kilometer) by region using linear models. Hind foot length differed between sexes and between regions. In 2 out of 3 regions, we observed a negative relationship between hind foot length and our index of roe deer density. Further, hind foot length was lower when springs (but not summers) were cold or wet. We interpreted these trends in relation to changes in population density and habitat structure. We concluded that hind foot length is a useful indicator for assessing the density-dependent relationship between roe deer populations and their environment and for monitoring population trends. (WILDLIFE SOCIETY BULLETIN 34(2):351–358; 2006)

Key words

body size, Capreolus capreolus, France, hind foot length, ecological indicator, linear models, population monitoring, roe deer, wildlife management.

Wildlife managers are increasingly under pressure to maintain an ecological and economical equilibrium between deer (Cervidae) populations and their environment (Warren 1997). Although deer play a natural role in ecological systems, they may have a negative impact at certain successional stages of commercial forest through browsing and grazing (Putman 1996). Consequently, wildlife managers require reliable information on population trends relative to habitat quality to set management objectives and adjust harvest quotas. Much of this information has been obtained using census methods (Caughley 1977, Seber 1982). However, estimation of population density in wilderness areas through surveys that are time-consuming and costly has proved to be neither accurate nor reliable (Williams et al. 2002).

For example, the roe deer (*Capreolus capreolus*) is a medium-sized ungulate that inhabits forest habitat, which makes it difficult to count (Andersen 1953, Strandgaard 1972). Traditional methods often underestimate abundance in a particular area, especially at high densities (Van Laere et al. 2001). Moreover, even the best estimates of population density may not provide enough information to manage deer populations. Concomitantly, population performance at a given density may differ by habitat types (Gaillard et al. 1996, Kjellander et al. 2006).

Managers require information on the number of deer that the habitat can sustain to assess the state of the equilibrium between the population and its environment. However, it is currently extremely difficult to quantify the availability of environmental resources and, hence, to infer accurately the optimal sustainable population (Pastor et al. 1997, del Monte-Luna et al. 2004). One solution to this dilemma may be the increased use of indicators of ecological change in management. Monitoring a set of indicators that reflect this equilibrium may provide an innovative approach on which to base management decisions (Cederlund et al. 1998).

Using this concept, researchers are developing new management tools for monitoring roe deer populations, rather than relying on often inaccurate and erroneous estimates of absolute density (Cederlund et al. 1998). Researchers have developed index methods that are sensitive to changes in population density (e.g., the kilometric index of abundance [Vincent et al. 1991], winter group size [Vincent et al. 1995]), environmental conditions (e.g., the browsing index [Morellet et al. 2001]) and the equilibrium between them (e.g., winter body mass of fawns [Gaillard et al. 1996], adult cohort jaw length [Hewison et al.

¹ E-mail: morellet@inra.toulouse.fr

1996], female fecundity [Vincent et al. 1995]). These indicators provide valuable information regarding the relationship between the population and its environment and thus are reliable tools for monitoring roe deer population trends.

These indices were designed for local use (i.e., a few thousand hectares). However, it is not always possible to apply management actions at such a fine scale. Most management units often are large with respect to the area inhabited by a deer population and decisions must be made at a larger scale (i.e., several thousand hectares). Hence, more effort and research are required to ascertain whether these indicators can be effective management tools at a landscape scale.

Body size of deer is influenced to a certain extent by genetic factors (Klein et al. 1987). Nevertheless, short-term variations in skeletal size within a single population are mainly due to environmental factors (Klein et al. 1987, Hewison et al. 1996). In particular, population density and climate are known to affect jaw size (Hewison et al. 1996) and leg length (Klein et al. 1987 for reindeer [*Rangifer tarandus*], Ashley et al. 1998 for white-tailed deer [*Odocoileus virginianus borealis*]) through their effects on forage quality and availability (Klein and Strangaard 1972, Klein et al. 1987).

Because deer hind feet grow rapidly after birth (Klein 1964) and cease growth early (Suttie and Mitchell 1983), we hypothesized that hind foot length would be sensitive to environmental conditions experienced by fawns. If correct, hind foot length could serve as an index of density-dependent limitation (the number of deer in relation to available resources) in roe deer populations.

Evidence suggests that hind foot length varies in a densitydependent manner at the local scale, reflecting variation in roe deer density in the enclosed population of the Chizé Reserve, western France (C. Toïgo, Office National de la Chasse et de la Faune Sauvage, Gienes, France, unpublished data). Accurate density estimates for this population are available from capturemark-recapture data (n = 901) collected from 1987 to 2003 to evaluate the relationship between roe deer fawn hind foot length and population density under controlled conditions (more or less constant habitat quality). Hind foot length decreased with increasing density in a similar way for both sexes (common slope $= -1.219 \pm 0.367$ (1 SE), $R^2 = 0.26$).

In this paper we report on a study we conducted on the variation in hind foot length of roe deer fawns over 13 years at the biogeographical scale of an entire French province. Specifically, we tested whether this variation was density dependent in order to assess whether this measurement could be used as a tool to monitor population trends and provide a basis for implementing management decisions at a landscape scale. To control for possible effects of environmental variation over the study period, we also investigated the relationship between hind foot length of roe deer fawns and an index of climatic variation (spring and summer precipitation and temperature). Hence, we considered climatic conditions as a proxy of variation in habitat quality over time.

Study Area

The study area was the Tarn province, southwestern France, which covers 5,796 km² and principally consists of hills and valleys. A range of mountains reaching 1,300-m in altitude lies to

the southeast. The climate is oceanic with some Mediterranean influences, characterized by mild temperatures (average yearly temperature of 13° C) and spring and autumn precipitation (average yearly precipitation of 760 mm). The southeastern part of the province is colder (average yearly temperature of 9.5° C) with more abundant precipitation (average yearly precipitation of 1,410 mm) due to mountain influences. All climatic data were obtained from Météo, France.

We divided the province into 3 regions based on forest cover and altitude (Fig. 1). To distinguish between forest and field areas, we used a Forest Numeric Model of the Tarn. We calculated a forest index from a Satellites d'observation de la Terre satellite image. We created a matrix of pixels of 50 m \times 50 m with a woodland code taking the values of either 0 (absence of woodland) or 200 (presence of woodland). Using a filtering function distance of 1 km, we then smoothed our matrix to give an index of the forest cover (see Hewison et al. 2001 for a similar approach) in which each pixel takes a value between 0 (completely open landscape) and 200 (totally forested landscape). Forest cover in the Tarn consisted of 72% deciduous trees and 28% coniferous trees (Inventaire Forestier National 1991). We defined region 1 (576 km²) as including the north and northwest of the province and comprising deciduous forest, dominated by oak (Quercus robur, Q. petraea, Q. ilex), chestnut (Castanea sativa), and beech (Fagus sylvatica). Region 2 (3,408 km²), situated in the central part of the province, principally consisted of farmed and urbanized land with little woodland. Region 3 (1,812 km²) was mountainous and covered the southeastern part of the province. It was a large mixed forest consisting of oak, chestnut, Norway spruce (Picea abies), Douglas-fir (Pseudotsuga douglassii), and true fir (Abies pectinata).

Roe deer and wild boar (*Sus scrofa*) were widespread over the entire province, while red deer (*Cervus elaphus*) were located in region 1 only. The total number of roe deer legally harvested in the entire province varied from 373 (0.06 shot roe deer/km²) to 4,999 (0.86 shot roe deer/km²) between 1990 and 2002.

Methods

Climatic Variables

We obtained monthly precipitation and average temperature from April to July from Météo, France, for 3 meteorological stations, 1 located in each of the 3 regions. We calculated a hydric index (HI) for spring (Apr and May) and for summer (Jun and Jul) as the average precipitation minus twice the mean temperature. This index reflects the availability of water for vegetation growth and is sensitive to droughts (Dajoz 1973). Because the hydric index is correlated with vegetation growth, it indicates the quantity of food available to roe deer in the spring vegetation flush, and the duration and quality of green forage in summer during the highenergy investment period of lactation to weaning. The quality and quantity of food availability in spring and summer is crucial for determining fawn growth (Kjellander et al. 2006). We therefore consider this index as providing a pertinent measure of variation in habitat quality over time for our study.

Data Collection

Wildlife managers of the Tarn Province collected left hind feet and report cards for all roe deer legally harvested in the province from 1990 to 2002 (n = 28,761). Gathering these data provided a



Figure 1. Map of the defined regions in the Tarn province, southwestern France, showing major roads, the Tarn River, and forested areas (gray shading).

way to regulate the application of harvest quotas and assess the usefulness of hind foot length as an indicator of ecological changes for monitoring roe deer populations. Hunters recorded sex, estimated age as fawns (<1 year old) or adults (>1 year old), and place and date of death. Hind feet were stored in freezers and sent to the Tarn Hunter Federation at the middle and at the end of the hunting season. All measurements were made by a single experienced wildlife manager with a wooden gauge to the nearest millimeter. The length of the outstretched hind foot was measured from the top of the calcaneum to the tip of the hoof (Fig. 2). From 1996 onwards, the hunter estimations of age were checked by looking at the layer of connecting cartilage that is present on the epiphyseal extremity of the metatarsus in fawns only. Navarre (1993) showed that this connecting cartilage disappeared at about 14-16 months of age in roe deer. Furthermore, he showed that it was a reliable method for distinguishing fawns and adults harvested during the hunting season from October to February.



Figure 2. Drawing of hind foot length measurement of a roe deer, measured from the extremity of the calcaneum to the tip of the hoof.

In the Tarn roe deer hunting occurred from 1 September to the beginning of February. During this period hunting consisted of drive-hunts with dogs (Boisaubert and Boutin 1988); thus, we assumed roe deer were harvested randomly with respect to sex, age, and body size. From 1990 to 2002, of 28,761 roe deer that were measured, 10,160 were classified as fawns.

Statistical Analysis

To perform the statistical analysis, we considered 2 data sets. First, to avoid taking into account adults which could be wrongly classified as fawns by hunters (prior to 1996), we selected fawns for which age had been identified from the cartilage method (i.e., after 1996). We obtained 6,701 fawns from 1996 to 2002 (sample 1). Second, we considered the whole sample, selecting years between 1990 and 2002 when at least 5 hind foot measurements of fawns were collected per region. Thus, we obtained 9,770 fawns harvested from 1993 to 2002: 1,109 in region 1; 2,267 in region 2; and 6,394 in region 3 (sample 2).

We assigned a Julian date to each hind foot length measurement running from 1 September (date 1) to 2 February (date 155) to include date of shooting in the model. To look for temporal and sexual variations of hind foot length of roe deer fawns, we tested for effects of year, sex, and date of shooting using an ANCOVA with year and sex as factors and date of shooting as a covariable. To avoid complex interactions that may be difficult to interpret we considered regions separately, building a model for each region. We compared values from ANCOVA tables and parameter estimates obtained using the confirmed age sample (sample 1) and the whole sample (sample 2). Because there were no notable differences, we chose to present the results obtained with the sample 2 only, thus increasing sample size and the number of years considered.

To examine the effects of climate and density on temporal variation of hind foot length of roe deer fawns, we adjusted hind foot length measurements to 15 November (date 76) which corresponded to the middle of the hunting season. We obtained coefficients for the adjustment from linear regressions of hind foot length on date of shooting, performed for each sex and each region. We then calculated the annual mean of adjusted hind foot length of roe deer fawns per region for males and females. We considered this annual measurement as our indicator.

We examined the effects of climate and density on the annual mean of adjusted hind foot length using an ANCOVA with sex as a factor and spring HI, summer HI, and an index of density as covariables in each region. We used the total number of harvested roe deer per square kilometer in each year and in each region as an index of density because there was no other reliable information on density of roe deer from 1993 to 2002 in the Tarn. This index is derived from the attribution of hunting quotas determined by a commission representing different organizations (hunters, forestry, local government, etc.) on the basis of field knowledge of deer abundance and on the success in achieving the previous year's quota in relation to hunting effort. Although the index is therefore likely to be an approximation, it undoubtedly reflects general population trends in deer density over time. However, it may be that yearly changes in our density measure could be somewhat imprecise. Hence, we performed an additional analysis based on 2 contrasted density periods: a low-density period (1993–1997) versus a high-density period (1998-2002). Based on the huge difference in mean yearly bag records between these periods (region 1: 0.33 ± 0.116 vs. 0.90 ± 0.109 ; region 2: 0.09 ± 0.048 vs. 0.31 \pm 0.062; region 3: 0.61 \pm 0.207 vs. 1.53 \pm 0.200 roe deer shot/km²), we can confidently assume that quotas reliably reflected contrasting abundance of roe deer between the 2 periods in each region. We then performed an ANCOVA for each region, including period (high vs. low density) and sex as factors with the summer and spring HIs as covariables in the model. To perform the analysis, we used SPSS version 11.5 (SPSS Inc., Chicago, Illinois) and R.2.0.1 (R Development Core Team 2004) software. We considered results significant when P < 0.05.

Results

Temporal and Spatial Variations of Hind Foot Length of Roe Deer Fawns

We classified our data by sex, region, and year. In a 3-way ANCOVA on hind foot length, the 3-way interaction sex-yeardate of shooting was not significant in 2 regions (region 1: $F_{9,1069}$ = 0.68, P = 0.731; region 2: $F_{9,2227} = 0.53$, P = 0.854). In these regions there was no sex-year interaction (region 1: $F_{9,1087} = 0.35$, P = 0.957; region 2: $F_{9,2245} = 1.10$, P = 0.357), no year-date of shooting interaction (region 1: $F_{9,1078} = 0.33$, P = 0.966; region 2: $F_{9,2236} = 0.79$, P = 0.622), and no sex-date of shooting interaction (region 1: $F_{1,1096} = 0.29$, P = 0.592; region 2: $F_{1,2254} = 0.59$, P =0.442). In contrast, in region 3 the 3-way interaction ($F_{9,6354} =$ 1.81, P = 0.062) and some 2-way interactions (sex-year: $F_{9,6364} =$ 1.86, P = 0.054; year-date of shooting: $F_{9,6373} = 1.88$, P = 0.051; sex-date of shooting: $F_{1,6363} = 2.31$, P = 0.129) were marginally nonsignificant. This result may reflect the higher statistical power in this region as the sample size was much larger than in the 2 others. However, in the absence of clear effects of interactions among factors with such high statistical power, we retained the additive model for region 3, as for the other 2 regions. From this model males had longer hind foot length than females (betweensex difference of 3.8 \pm 0.8 mm, $F_{1.1097} = 21.91$, $P \le 0.001$; of 4.1 \pm 0.5 mm, $F_{1,2255} = 60.72$, $P \leq 0.001$; and of 3.5 \pm 0.4 mm, $F_{1,6382} = 94.23, P \le 0.001$ in regions 1, 2, and 3, respectively). Hind foot length of roe deer fawns differed among years, generally showing a pattern of decrease over the period considered (from 317.6 in 1993 to 310.2 mm in 2002, $F_{9,1097} = 2.36$, P = 0.012; from 317.3 in 1997 to 312.5 mm in 2002, $F_{9,2255} = 3.34$, $P \leq$ 0.001; from 313.2 in 1995 to 308.2 mm in 2001, $F_{9.6382} = 7.36$, P \leq 0.001 in regions 1, 2, and 3, respectively; Fig. 3). Lastly, hind foot length increased by 0.110 (\pm 0.011), 0.138 (\pm 0.007), and $0.108 (\pm 0.005) \text{ mm/day over the hunting season in region 1}$ $(F_{1,1097} = 103.51, P \le 0.001)$, region 2 $(F_{1,2255} = 395.28, P \le 0.001)$ 0.001), and region 3 ($F_{1,6382} = 541.28$, $P \le 0.001$), respectively.

Because there was no significant interaction between sex, year, and date of shooting in any of the 3 regions, while there were significant effects of date of shooting and sex, we adjusted hind foot length measurements to 15 November (date 76), which corresponded to the middle of the hunting season, and we retained sex as an additive factor in all following models.

Relation of Mean Adjusted Hind Foot Length of Roe Deer Fawns with Climate and Density

To test whether hind foot length could be a reliable indicator of ecological changes, we investigated the relationship between annual mean hind foot length, our hydric index of spring and summer climate, and our index of population density while controlling for between-sex differences. Because the aim of ecological indicators is to monitor population trends over time in a specific management unit, comparisons between regions are not relevant. Hence, we performed a separate ANCOVA for each region. The density of harvested roe deer increased from 1993 to 1999. It then stabilized in region 2, while it decreased slightly in regions 1 and 3 (Fig. 4).

Neither the 4-way interaction (density-spring HI-summer HIsex) nor any of the 3-way interactions were significant in the 3 regions. In region 1, there was a significant interaction between our index of density and spring HI ($F_{1,15} = 12.72$, P = 0.003), indicating that hind foot length responds differently to environmental variations depending on the level of population density. Males had longer hind foot length than females ($F_{1,15} = 22.61$, P = 0.004, a between-sex difference of 3.25 ± 0.68 mm). To explore the spring HI-density interaction, we considered 2 classes of spring HI, contrasting wet, cold springs with dry, warm ones. For both these classes of spring HI, annual mean hind foot length of roe deer fawns was negatively related to our index of density (Fig. 5). Hind foot length appeared to be more sensitive to density for low values of spring HI (Fig. 5). In region 2, there was a significant interaction between spring HI and sex ($F_{1,15} = 6.36$, P = 0.023) such that hind foot length of males decreased with increasingly wet and cool springs (slope = -0.071 ± 0.02), whereas it did not vary for females (slope = 0.00 ± 0.01). There was no significant effect of the density index on hind foot length











Figure 3. Mean hind foot length (in mm) of female (in grey) and male (in black) roe deer in 3 regions of the Tarn province, southwestern France, from 1993 to 2002. Bars indicate a 95% confidence interval for the mean.

 $(F_{1,15} = 2.15, P = 0.163)$. Males had longer hind foot length than females (between-sex difference of 4.5 \pm 0.74 mm; Fig. 5). In region 3, annual mean hind foot length of roe deer fawns differed between sexes ($F_{1,17} = 28.35, P \le 0.001$, between-sex difference of 3.18 \pm 0.55 mm) and was negatively related to the index of density ($F_{1,17} = 17.80, P \le 0.001$, slope = -2.77 ± 0.56 ; Fig. 5). Hind foot length tended to decrease with increasing spring HI for males ($F_{1,16} = 4.26, P = 0.055$, slope = -0.017 ± 0.01) and did not vary for females (slope = 0.00 ± 0.02). In all 3 regions, summer HI did not influence hind foot length of roe deer fawns



Figure 4. Number of shot roe deer per square kilometer in 3 regions of the Tarn province, southwestern France, from 1993 to 2002.

(region 1: $F_{1,14} = 1.62$, P = 0.223; region 2: $F_{1,14} = 3.87$, P = 0.069; region 3: $F_{1,15} = 0.10$, P = 0.750).

We found similar results when considering 2 contrasted density periods. In region 1, after exclusion of nonsignificant interactions, hind foot length was 3.20 ± 0.87 mm lower during the highdensity period compared to low-density period ($F_{1,17} = 13.44$, P =0.002). Males had longer hind foot length than females ($F_{1,17} =$ 13.92, P = 0.001, between-sex difference of 3.25 ± 0.87 mm). Neither spring nor summer HI influenced hind foot length of roe



Figure 5. Relationship between annual mean hind foot length (in mm) of female and male roe deer fawns and the number of shot roe deer per square kilometer in 3 regions of the Tarn province, southwestern France. Low (A1) and high (A2) values of spring hydric index (HI) in region 1, (B) region 2, and (C) region 3.

deer fawns ($F_{1,17} = 0.00$, P = 0.991 and $F_{1,15} = 0.93$, P = 0.350, respectively). In region 2, there was a significant interaction between sex and spring HI ($F_{1,16} = 5.08$, P = 0.038). There was no significant relationship between hind foot length and the index of density ($F_{1,15} = 2.55$, P = 0.131) and between hind foot length and summer HI ($F_{1,14} = 3.53$, P = 0.081). In region 3, we retained an additive model including sex ($F_{1,17} = 24.97$, P < 0.001) and the index of density ($F_{1,17} = 13.65$, P = 0.002). Hind foot length was 2.35 ± 0.63 mm lower during the high-density period compared to low-density period. There was no significant effect of climate on hind foot length for this region (spring HI: $F_{1,15} = 0.68$, P =0.421; summer HI: $F_{1,16} = 0.95$, P = 0.344).

Discussion

We investigated the relationship between hind foot length of roe deer and an index of density to assess the usefulness of hind foot length for identifying density-dependent population trends and determining management strategy at a landscape scale. We controlled for possible environmental variation over time by including measures of spring and summer climatic variation in the analysis. We found a negative relationship between hind foot length and our index of density in regions 1 and 3, indicating a density-dependent response and suggesting that hind foot length could be a useful indicator for monitoring the relationship between the deer population and its environment. However, no significant relationship could be detected in region 2. This result might be due to the fact that deer density was low in this region and the population might not yet have reached the threshold where density-dependent limitation occurs.

In this study, hind foot length showed a consistent pattern of decline over the years over the whole province due to increasing density and climatic variation, despite some oscillations in certain years (Fig. 3). This result indicates that monitoring of biological indicators must be considered over a long period of time in order to detect trends. The increase of bag records from 373 to 4,999 in 10 years as population density increased at our study site corresponds to a sustained natural rate of increase of about 1.33, which roughly corresponds to the rate of increase observed in French roe deer populations during the colonization phase (Gaillard et al. 1992). Although we did not expect this index of density to closely track the real fluctuations of population density, we are confident that variations reflect real trends of population density at a coarse scale. In support of this, whether we used annual variations of this index of density or simply 2 contrasted periods we obtained the same results.

Population density (Klein et al. 1987, Hewison et al. 1996, Ashley et al. 1998), climatic conditions (Gaillard et al. 1996, Post et al. 1997), and habitat quality (Bertouille and De Crombrugghe 1995, Hewison et al. 1996) are factors involved in short-term changes of body size and condition of deer within a population. Results from several studies on leg length of reindeer and caribou, reviewed by Klein et al. (1987), noted that skeletal development depended primarily on nutritional conditions experienced by animals, which depended on both population density and climatic regimes. Gaillard et al. (1996) studied body mass of roe deer fawns in 2 reserves with contrasting climatic conditions and found a negative relationship between April–May precipitation and body mass of fawns. This is in agreement with our study, as hind foot length was lower (region 1 for both sexes, regions 2 and 3 for males) at high values of spring HI, that is, during cool, wet springs. The negative impact of spring hydric conditions on fawn hind foot length contrasts with the absence of any influence of summer hydric conditions. This suggests that roe deer fawns in the 3 regions were more sensitive to the quantity of food available during the spring and the beginning of the summer than to the duration of green forage and its quality.

We also observed differences in hind foot length between the regions. These differences could be explained by several factors such as differences in population density, forage quality, and habitat structure. This spatial heterogeneity underlines the fact that the comparison of indicator values are appropriate only within a given area (i.e., longitudinal trends rather than spatial comparisons) because a given population responds differently in relation to its environment. Even so, we found the smallest roe deer in the area of highest density, region 3, which is a forested and mountainous region with relatively harsh environmental conditions. Indeed, this region is the wettest and coolest in the province (average spring HI of 88 vs. 60 in regions 1 and 2). In region 1, hind foot length was intermediate, while we found the biggest fawns in the cultivated zone (region 2) where the index of population density was the lowest. Previously, Klein and Strandgaard (1972) indicated that small roe deer in Denmark were found in areas with intensive agriculture, low forest-toagriculture land ratio and high deer densities. In contrast, Fruzinski et al. (1982) compared morphometric parameters of forest and field roe deer and showed that field roe deer were larger than forest roe deer, presumably because of the higher quantity of available food. Our results are consistent with those of Fruzinski et al. (1982) because fawns from region 2 had longer hind foot length than fawns from regions 1 and 3. It seems that environmental variation in terms of climate was more important than density dependence in determining fawn growth in this region, probably because deer density was low.

Sexual dimorphism is low in roe deer (Hewison et al. 2002). No sex differences were recorded for birth weight (Gaillard et al. 1993), for early growth rate (Portier et al. 2000), or for postweaning growth (Hewison et al. 2002) in this species. In our study hind foot length of males and females differed slightly but significantly, indicating that comparisons of morphometric data should take sex into account.

Management Implications

Deer are key species in forest ecosystem functioning (Kuiters et al. 1996). As a consequence, wildlife management should be concerned with ecosystem management at a large scale. Roe deer hind feet were easily collected over the entire province and, therefore, provided information at a landscape scale more suitable for population management than typical management units. It took approximately 1 hour for an experienced wildlife manager to measure 150 hind feet. In addition, the examination of the connecting cartilage on the epiphyseal extremity of the metatarsus provides a reliable way to distinguish fawns from adults (Navarre 1993). However, to be able to deduce population trends and adjust management plans, it is necessary to simultaneously monitor

several indicators of ecological change that provide information on the different components of the population-environment system. Integrating information on hind foot length with other indices, such as the browsing index (Morellet et al. 2001) and the kilometric index (Vincent et al. 1991), would provide a comprehensive picture of the relationship between the roe deer population and its environment. Indeed, the observed decline in hind foot length over the study period does not provide information on the cause of that change, that is, whether the decline is due to lower habitat quality or increased population abundance. However, information on the mechanism driving such change may be less important for a wildlife manager than having a reliable indicator of density dependence that will affect life-history

Literature Cited

- Andersen, J. 1953. Analysis of the Danish roe deer population based on the extermination of the total stock. Danish Review of Game Biology 2:127–155.
- Ashley, E. P., G. B. McCullough, and J. Robinson. 1998. Morphological responses of white-tailed deer to a severe population reduction. Canadian Journal of Zoology 76:1–5.
- Bertouille, S. B., and S. A. De Crombrugghe. 1995. Body mass and lower jaw development of the female red deer as indices of habitat quality in the Ardennes. Acta Theriologica 40:145–162.
- Boisaubert, B., and J. M. Boutin. 1988. Le chevreuil. Hatier, Paris, France.
- Caughley, G. 1997. Analysis of vertebrate populations. John Wiley and Sons, London, United Kingdom.
- Cederlund, G., J. Bergqvist, P. Kjellander, R. B. Gill, J.-M. Gaillard, B. Boisaubert, P. Ballon, and P. Duncan. 1998. Managing roe deer and their impact on the environment: maximising the net benefits to society. Pages 337–372 *in* R. Andersen, P. Duncan, and J. D. C. Linnell, editors. The European roe deer: the biology of success. Scandinavian University, Oslo, Norway.
- Dajoz, R. 1973. Précis d'écologie. Gauthier, Villars, France.
- del Monte-Luna, P., B. W. Brook, M. J. Zetina-Rejón, and V. H. Cruz-Escalona. 2004. The carrying capacity of ecosystems. Global Ecology and Biogeography 13:485–495.
- Fruzinski, B., J. Kaluzinski, and J. Baksalary. 1982. Weight and body measurements of forest and field roe deer. Acta Theriologica 27:479–488.
- Gaillard, J.-M., D. Delorme, J. M. Boutin, G. Van Laere, and B. Boisaubert. 1996. Body mass of roe deer fawns during winter in two contrasting populations. Journal of Wildlife Management 60:29–36.
- Gaillard, J.-M., D. Delorme, and J. M. Jullien. 1993. Effects of cohort, sex and birth date on body development of roe deer (*Capreolus capreolus*) fawns. Oecologia 94:57–61.
- Gaillard, J.-M., J. D. Lebreton, D. Pontier, and P. Landry. 1992. Demographic sensitivity and population management: an application to roe deer (*Capreolus capreolus*). Pages 547–550 *in* Eighteenth Congress of International Union of the Game Biologists, 23 August 1987, Cracovia, Poland.
- Hewison, A. J. M., J.-M. Gaillard, J. M. Angibault, G. Van Laere, and J. P. Vincent. 2002. The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. Journal of Zoology 257:303–309.
- Hewison, A. J. M., J. P. Vincent, E. Bideau, J. M. Angibault, and R. J. Putman. 1996. Variation in cohort mandible size as an index of roe deer (*Capreolus capreolus*) densities and population trends. Journal of Zoology 239:573– 581.
- Hewison, A. J. M., J. P. Vincent, J. Joachim, J. M. Angibault, B. Cargnelutti, and C. Cibien. 2001. The effect of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. Canadian Journal of Zoology 79:679–689.
- Inventaire Forestier National. 1991. Troisème cycle. Département du Tarn, Montpellier, France.
- Kjellander, P., J.-M. Gaillard, and A. J. M. Hewison. 2006. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521–530.
- Klein, D. R. 1964. Range-related differences in growth of deer reflected in skeletal ratios. Journal of Mammalogy 45:226–235.

traits of individuals and, hence, population dynamics. As hind foot length reflects the interaction between habitat quality and population abundance, we believe it provides an objective assessment of the level of density-dependent limitation of a roe deer population. Such index methods are less time-consuming and costly than counting methods and more useful for making management decisions because they provide us with reliable information on populations trends in relation to their environment.

Acknowledgments

We thank J. Joachim for drawing Fig. 1, and S. Aulagnier and P. Kjellander for comments on an earlier version of this manuscript.

- Klein, D. R., M. Meldgaard, and S. G. Fancy. 1987. Factors determining leg length in *Rangifer tarandus*. Journal of Mammalogy 68:642–655.
- Klein, D. R., and H. Strandgaard. 1972. Factors affecting growth and body size of roe deer. Journal of Wildlife Management 36:64–79.
- Kuiters, A. T., G. M. J. Mohren, and S. E. Van Wieren. 1996. Ungulates in temperate forest ecosystems. Forest Ecology and Management 88:1–5.
- Morellet, N., S. Champely, J.-M. Gaillard, P. Ballon, and Y. Boscardin. 2001. The browsing index: new tool uses browsing pressure to monitor deer populations. Wildlife Society Bulletin 29:1243–1252.
- Navarre, P. 1993. Distinction des chevrillards et des chevreuils (*Capreolus capreolus*) de plus d'un an par examen du métacarpe ou de métatarse. Gibier Faune Sauvage 10:135–142.
- Pastor, J., R. Moen, and Y. Cohen. 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal–landscape interactions. Journal of Mammalogy 78:1040–1052.
- Portier, C., P. Duncan, J.-M. Gaillard, M. Guillon, and A. J. Sempere. 2000. Growth of European roe deer: patterns and rates. Acta Theriologica 45:87– 94.
- Post, E., N. C. Stenseth, R. Langvatn, and J. M. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. Proceedings of the Royal Society of London 264:1317–1324.
- Putman, R. J. 1996. Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. Forest Ecology and Management 88:205–214.
- R Development Core Team. 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed 2006 Feb 22.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Griffin, London, United Kingdom.
- SPSS Inc. 1999. SPSS Base 10.0 for Window's User's Guide. SPSS Inc., Chicago, Illinois.
- Strandgaard, H. 1972. The roe deer (*Capreolus capreolus*) population at Kälo and the factors regulating its size. Danish Review of Game Biology 7:1–205.
- Suttie, J. M., and B. Mitchell. 1983. Jaw length and hind foot length as measures of skeletal development of red deer (*Cervus elaphus*). Journal of Zoology 200:431–434.
- Van Laere, G., D. Maillard, D. Delorme, and J.-M. Gaillard. 2001. Roe deer population census using the observation sector approximation method: a reliability test. Mammalia 65:240–244. [In French.]
- Vincent, J. P., E. Bideau, A. J. M. Hewison, and J. M. Angibault. 1995. The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). Journal of Zoology 236:371–382.
- Vincent, J. P., J.-M. Gaillard, and E. Bideau. 1991. Kilometric index as a biological indicator for monitoring forest roe deer populations. Acta Theriologica 36:315–328.
- Warren, J. 1997. The challenge of deer overabundance in the 21st century. Wildlife Society Bulletin, special issue 25:213–215.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.



Audrey Zannèse (photo) obtained her Master of Analysis and Modeling of Biological Systems from Université Claude-Bernard – Lyon I in 2004. She is currently doing her Ph.D. at the University of Leeds. She is interested in population dynamics and particularly in spatial population synchrony. **Jean-Michel Gaillard** is a population ecologist working at the Research Unit of Biometry and Evolutionary Biology at the Centre National de la Recherche Scientifique, Lyon, France. He obtained his Ph.D. in 1988 and his Habilitation à Diriger des Recherches in 1994 from Université Claude-Bernard at Lyon.

His main research interests include the evolution of life-history strategies in vertebrates, population dynamics of large herbivores, patterns of maternal care in large herbivores, and population monitoring. Mark Hewison is a population ecologist working at the CEFS laboratory (Behaviour and Ecology of Wildlife) at the Institut National de la Recherche Agronomique, Toulouse, France. He obtained his Ph.D. from Southampton University in 1993 and his Habilitation à Diriger les Recherches from Université Paul Sabatier in 1999. He is particularly interested in life-history strategies and spatial ecology of ungulates in relation to landscape structure. Karine Saint-Hilaire and Alain Baisse are wildlife managers working, respectively, in the Fédération Régionale des Chasseurs Midi-Pyrénées and Fédération Départementale des Chasseurs du Tarn. Both are heavily involved in the management of game species. Carole Toigo is a wildlife biologist working at the Office National de la Chasse et de la Faune Sauvage, Gières, France. She obtained her Ph.D. on biodemographic strategies of alpine ibex from the Université Claude-Bernard - Lyon I in 1998. She is particularly interested in ungulate population dynamics. Guy Van Laere is a game and wildlife technician. He is working at the Office National de la Chasse et de la Faune Sauvage, on the Réserve Nationale de Chasse et de Faune Sauvage de Chizé, since 1978. He is particularly interested in the monitoring and management of ungulate populations, especially roe deer. Nicolas Morellet is a population ecologist working at the CEFS laboratory (Behaviour and Ecology of Wildlife) at the Institut National de la Recherche Agronomique, Toulouse, France. He obtained his Ph.D. from Université Claude-Bernard - Lyon I in 1998. He is particularly interested in the monitoring of ungulate populations and their habitat use.

Associate Editor: Krausman.