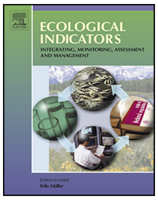
Ecological Indicators 45 (2014) 300–307

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Eruption patterns of permanent front teeth as an indicator of performance in roe deer

Mathieu Garel[a,c,*], Jean-Michel Gaillard[b], Daniel Delorme[c], Guy Van Laere[c]

[a] Office National de la Chasse et de la Faune Sauvage, Centre National d'Études et de Recherche Appliquée Faune de Montagne, 5 allée de Bethléem, Z.I. Mayencin, 38610 Gières, France
[b] Laboratoire de Biométrie et Biologie Évolutive, UMR-CNRS 5558, Université de Lyon, Univ. Lyon 1, 69622 Villeurbanne Cedex, France
[c] Office National de la Chasse et de la Faune Sauvage, Centre National d'Études et de Recherche Appliquée Cervidés-Sanglier, 1 Place Exelmans, F-55000 Bar-le-Duc, France

ARTICLE INFO

Article history:
Received 24 May 2013
Received in revised form 21 February 2014
Accepted 25 March 2014

Keywords:
Body mass
Capreolus capreolus
Density-dependence
Front teeth
Indicators of ecological changes
Wildlife management

ABSTRACT

In most species of vertebrates, teeth play a central role in the long-term performance of individuals. However, patterns of tooth development have been little investigated as an indicator of animal performance. We filled this gap using data collected during long-term capture-mark-recapture monitoring of 1152 roe deer fawns at Chizé, western France. This population fluctuated greatly in size during the 27 years of monitoring, offering a unique opportunity to assess how the eruption patterns of front teeth perform as indicator of animal performance. We used three indices of the eruption of permanent front teeth, the simplest being whether or not incisor I_2 has erupted, and the most complex being a 12-level factor distinguishing the different stages of tooth eruption. We also assessed the relevance of these indices as compared to fawn body mass, a widely used indicator of animal performance of deer populations. Dental indices and body mass were positively correlated (all $r > 0.62$). Similarly to body mass, all indices based on tooth eruption patterns responded to changes of population size and can be reliably used to assess the relationship between roe deer and their environment. We found a linear decrease in body mass with increasing population size ($r^2 = 0.54$) and a simultaneous delay in tooth development ($r^2 = 0.48$–0.55 from the least to the most accurate indicator). However, tooth development would be not further delayed in years with the highest densities (>15 adult roe deer/100 ha). A path analysis supported the population density effect on tooth eruption patterns being mainly determined by the effect of population size on body mass. Our study provides managers with simple indices (*e.g.*, presence-absence of I_2) that provide a technically more easy way to standardize measurements of deer density-dependent responses over large geographical and temporal scales than would be possible with body mass.

1. Introduction

Populations of large herbivores are commonly (*e.g.*, in North America, Western Eurasia) controlled through hunting using yearly quotas (Gordon et al., 2004). Quotas are often determined using estimates, or indices, of population density as a proxy for demographic status (Williams et al., 2002). Management decisions are then based on the observed population changes between consecutive years. This approach has recently been challenged because counting large herbivores is an especially difficult task (Caughley, 1977) and includes problems of both limited accuracy and poor precision (Morellet et al., 2007). Furthermore, monitoring only population abundance does not provide any information on the relationship between the focal population and its habitat. Morellet et al. (2007) have therefore proposed that managers should consider changes in both population parameters and habitat characteristics, as well as their interaction, for successful management of ungulate populations. These changes can be monitored through indicators of ecological change (*sensu* Cederlund et al., 1998) including indicators of animal performance (*e.g.*, Bonenfant et al., 2002; Gaillard et al., 1996; Garel et al., 2011b; Strickland et al., 2008), relative measure of animal abundance (*e.g.*, Garel et al., 2010; Loison et al., 2006; Vincent et al., 1991), assessment of habitat quality and/or evaluation of the impact of large herbivores on

---

Abbreviations: BM, body mass; DFI, dental formula index; PFTI, permanent front tooth index.

[*] Corresponding author at: Office National de la Chasse et de la Faune Sauvage, Centre National d'Études et de Recherche Appliquée Faune de Montagne, 5 allée de Bethléem, Z.I. Mayencin, 38610 Gières, France. Tel.: +33 476 59 32 07.

E-mail address: mathieu.garel@oncfs.gouv.fr (M. Garel).

http://dx.doi.org/10.1016/j.ecolind.2014.03.025
1470-160X/

habitat structure and composition (Chevrier et al., 2012; Morellet et al., 2001). Simultaneously monitoring temporal changes in these ecological indicators provides an adaptive way for setting hunting quotas and for achieving specific management objectives.

Using indicators of ecological changes to monitor populations of large herbivores typically rely on interpreting the functional relationship between a biological parameter and the changes in population size. Thus, monitoring density-dependence provides a way to measure population-habitat relationships and all parameters that respond to changes in relative density (*i.e.*, changes in population size for a given habitat quality) can be viewed as candidate ecological indicators. So far, juvenile and yearling body mass correspond to the ecological indicators of animal performance that are most often used to monitor the status of ungulate populations in relation to habitat quality (*e.g.*, Bonenfant et al., 2002; Gaillard et al., 1996; Garel et al., 2011b; Strickland et al., 2008). Body size has also been found to be a reliable indicator of animal performance in roe deer (*Capreolus capreolus*; Hewison et al., 1996; Zannèse et al., 2006). Recently, it has been shown that body mass and hind foot length display different density-dependent responses: hind foot length is less sensitive to density than body mass and decreases with increasing density only when environmental conditions become very harsh (Toïgo et al., 2006). Monitoring indicators based on body development could improve the reliability of assessments of the relationship between a population and its habitat along the colonization-saturation continuum by describing the full range of variation in density for a given population.

Developing alternative indicators to body mass presents other advantages. First, body mass is prone to sampling variation caused by varying degrees of fullness of the digestive tract or loss of body fluids, and large seasonal variation (*e.g.*, caused by rutting activities in males, see Garel et al., 2011a; Leader-Williams and Ricketts, 1982). Precision of measurements has implications in terms of monitoring because imprecise measurements should require an increased sample size to detect biological signals. Second, monitoring growth patterns of a part of the animal body (*e.g.*, hind foot length) is an interesting alternative for collecting data (see Zannèse et al., 2006 for an example of hind feet collected over large spatio-temporal scales by hunters) and for standardizing measurements (with the simultaneous increase of precision). Focusing on such biological indicators enables data to be collected from part rather than the whole animal; sampling the whole animal can be difficult if the animal is large or if hunters take only part of the animal (*e.g.*, head).

In this context, monitoring tooth eruption patterns could be a biological and technical relevant alternative for monitoring populations of large herbivores, although it has been poorly investigated up to now despite the central role of teeth in the life history of large herbivores. Previous studies in deer species have shown that eruption of permanent teeth is delayed in young animals under food restriction (Robinette et al., 1957) and increasing local density (Loe et al., 2004); and similar patterns have been reported in human populations (Garn et al., 1965). These results suggest that tooth eruption patterns could be used as an indicator of animal performance (*sensu* Morellet et al., 2007). Two density-dependent responses in tooth eruption could be expected. First, like body mass growth (*e.g.*, Garel et al., 2011b; Toïgo et al., 2006), tooth eruption can be delayed at high density (H1). Second, because of their functional role in acquiring and chewing food as a preparation for digestion, teeth may have different growth priority as compared to body mass, and we may therefore expect different responses of teeth to food restriction compared to body mass response (H2). Tooth eruption should have a higher priority than growth of muscle or fat tissue and should therefore be less affected by nutritional deficiencies in the diet than total body mass (H2a), *i.e.*, body mass is expected to decrease first, whereas tooth eruption pattern should be quite stable and would start to be delayed only under very harsh environmental conditions (Klein, 1964; Toïgo et al., 2006). Alternatively, tooth eruption may start to be delayed simultaneously with body mass because both are interrelated (Kaur and Singh, 1992) but may cease to be delayed under very harsh environmental conditions because of their functional role in food intake (H2b). In both cases, monitoring of tooth eruption patterns and body mass concurrently should thus provide a meaningful signal of populations facing with changing environmental conditions.

The roe deer is a widespread and abundant ungulate species in Eurasia and is a highly-valued game species for which monitoring tools are required by managers (Cederlund et al., 1998). We studied a population of roe deer intensively monitored by capture-mark-recapture for 27 years, which experienced large variation in population size (Fig. 1 and Table 4). This long-term monitoring offers a unique opportunity to assess both the relevance of tooth eruption patterns to identify the relationships between roe deer and their environment (H1), and the existence of a different growth priority of tooth eruption compared to growth in body mass (H2a,b). We focused on the eruption patterns of permanent front teeth because ungulate population dynamics has been reported to be mostly sensitive to early performance (Gaillard et al., 2000). In addition, annual changes in animal performance of younger-aged individuals are the best indicator of changes of animal density along the colonization-saturation continuum (Bonenfant et al., 2009). We analyzed 3 indices of eruption patterns of permanent front teeth, with the simple one being whether or not incisor I_2 has erupted and for the most complex one a 12 level factor distinguishing the different stages of tooth eruption. Indeed, we aimed at providing managers with tooth indices that can be easily standardized and measured over large geographical and temporal scales at which management operates. Lastly, we used a path analysis (Shipley, 2002) to quantify to what extent density effects on tooth eruption pattern operate through body mass or might also result from direct effects of density on tooth development (Loe et al., 2004).

2. Materials and methods

2.1. Study area

We studied the roe deer population in the Chizé wildlife reserve (2614 ha), western France (46°05′N, 0°25′W).The climate is oceanic with Mediterranean influences, mild winters, and warm and often dry summers. This fenced reserve managed by the Office National des Forêts (ONF) consists of a forest dominated by oak (*Quercus* sp.) and beech (*Fagus sylvatica*) with low productivity because of infertile soils and frequent summer droughts. High variation in population size (controlled by yearly removals; Fig. 1, Table 4; from 165 to 512 roe deer, mean = 315, standard deviation = 100) offers highly contrasted conditions to test our biological hypotheses (H1–H2a,b).

2.2. Data

The Chizé population has been intensively monitored using capture-mark-recapture methods since 1977. Roe deer are caught annually between October and March (mostly in January–February) using drive netting (*i.e.*, about 5 km of vertical nets per capture day, 10–12 capture days per year), a method approved by the French Environment Ministry (articles L.424–1, R.411–14 and R.422–87 of the French code of environment). In addition, newborns are ear-tagged during the fawning period (May–June, Gaillard et al., 1993). A high proportion of the population (~70%) was individually marked during most years and allowed obtaining reliable estimates of yearly adult population size (> 1 year of age in March) using a generalization of the Cormack–Jolly–Seber model (Gaillard et al., 1986). During the study period, the population fluctuated markedly due to variation in both yearly removals and density-dependent responses