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Technical note

The effect of animal density on metacarpus development in captive fallow deer

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Abstract

During the development of mammals, skeletal growth is an informative measure of homeostasis between environmental conditions and individual anabolism. Young animals are more sensitive to adverse conditions than adults because they invest the majority of their resources in somatic growth. Here, by means of a manipulative experience, we aim to explore the effect of density oscillations on skeletal development as measured by the age of ossification and the total length of the metacarpus in juvenile fallow deer (*Dama dama* Linneaus, 1758) inhabiting an enclosure (south-western France). Our results show that, for animals born at high density, the total length of the metacarpus was lower on average by about 11.2 mm for females and 9 mm for males compared to animals born in low-density conditions. Furthermore, we observed that the age of ossification of both sexes was earlier in animals that experienced high density during early growth (5.8 months for females and 7.7 months for males at high density *versus* 12 and 12.8 months, respectively at low density). The total length of metacarpi and the age of ossification did not differ between the sexes in both high- and low-density periods. We conclude that the length of bones and the age at which animals achieve total ossification is sensitive to changes in animal's density, probably because of density-dependent competition for resources.

Keywords: *Dama dama*; Epiphysis; Growth; Metacarpus; Ossification; Population density

1. Introduction

The growth rate of an animal is an indicator of the equilibrium between assimilated energy and the development of the musculoskeletal system. A shortage of resources is particularly important during the first phases of development, from the foetal stages (Robinson, 1977) to the post-natal growth stage (Tudor et al., 1980), because the organism must invest the majority of available energy for increasing its size and weight.

During growth, nutrients are generally partitioned to various tissues of the animal, in priority order according to their metabolic rate. The work of Wallance (1948) showed that during active growth, certain tissues mature before others; for example, growth begins with neural tissue and proceeds to bone, muscle tissue, organs and adipose tissue. Endochondral ossification, the process which facilitates skeletal development in mammals, is characterised by the apparition of an intermediary hyaline cartilage which is gradually ossified until it is transformed to mature bone. In long bones this process starts with the apparition of two ossification centres (metaphysis and diaphysis) connected by the epiphyseal growth plate, which remains present until bone growth is complete (Carter et al., 1991).

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During the early stages, the genetic complex Hox is considered the principal protagonist in determining skeletal development, but later ossification is widely influenced by endogenous (growth hormone, insulin-like growth factors, thyroid hormone, glucocorticoids, steroids and Vitamin D) and exogenous (mechanical forces, energetic availability, protein balance, Ca/P equilibrium, and Vitamins A and C) factors (Nap and Hazewinkel, 1994).

In healthy animals, it is well known that skeletal growth and body condition are negatively affected by increasing animal density and scarcity of resources in both farmed (Tudor et al., 1980; Owens et al., 1993) and wild (Choquenot, 1991; Leberg and Smith, 1993; Ferguson et al., 2000; Hewison et al., 2002) ungulates.

In fallow deer adult males are 40% heavier than adult females (Chapman and Chapman, 1997). In many polygynous ungulates, where males are much larger than females, a potential consequence of sexual dimorphism is that males and females may respond differently to stressful environmental conditions, with males generally more affected than females (Clutton-Brock et al., 1982; Leberg and Smith, 1993). Few studies have experimentally tested *in situ* the effects of high-ungulate density on body development, because of the difficult of performing manipulative experiments on large mammals (Verme and Ozoga, 1980; Stewart et al., 2005). Even fewer studies have studied how the age of ossification is influenced by limiting environmental conditions (Lewall and Cowan, 1963; Purdue, 1983).

Our aim here is to investigate the effect of density on the development and ossification of the metacarpus in an enclosed group of fallow deer in south-western France. By means of visual inspection of ossification stage and osteometrical measures of the metacarpi, we aimed to investigate: the effect of high-animal density on (1) the total length of the metacarpus and (2) the age of ossification of the distal epiphysis. Because fallow deer are sexually dimorphic, in the analysis we controlled for differences between the sexes.

2. Materials and methods

2.1. Study animals

In 1980, a total of seven fallow deer (five from a neighbouring region and two from Scotland) were released in an enclosure of 130 ha situated in the Forêt Domaniale of Buzet northeast of Toulouse, France (43°46′N, 1°35′E). These animals were regularly monitored from 1988 to 1995, for research purposes by the CEFS (Laboratoire de Comportement et Ecologie de la Faune Sauvage, INRA). Animals were captured by chemical immobilization and marked with a leather collar with a colour code. While anaesthetized, each animal was weighed and sexed. The majority of animals were captured as fawns and yearlings and their age was assigned in months, considering the 1st June as the most common birth date in this enclosure (more than 80% of recorded births took place between 1 and 10 June, $n = 20$). Adult animals were aged by the tooth replacement technique (Chapman, 1990). The total number of individuals was known precisely from the founding of the enclosure by means of an exhaustive census. From the first seven animals released (5.4 individuals/km^2) the fallow deer group grew to 120 individuals (92 individuals/km^2) (Vicent et al., 1996). For management purposes 68% of animals was culled in the winter of 1993 (high-density period), and then most of the rest were eliminated during the two following winters. Due to these removals, the number of animals in the enclosure decreased to 38 individuals in 1994 and finally 30 in 1995 (low-density period). The average density for the years 1994–1995 was estimated as 23 individuals/km^2 (Vicent et al., 1996). Because the area was fenced and additional food was supplied only occasionally, we assume that during conditions of high-density food resources were scarcer and probably limiting compared to conditions of low density.

2.2. Bone preparation

We studied a total of 59 metacarpi of fallow deer (*Dama dama* Linnaeus, 1758): 26 females and 33 males with ages ranging from 0.5 to 67 months. Soft tissues were removed from fresh metacarpus before boiling in a 1% potassium hydroxide (KOH) solution. The total length of the right metacarpus was measured according to von den Driesch (1976) and the stages of ossification were assigned according to (Serrano et al., 2006).

2.3. Statistical analysis

In order to analyse the effect of animal density on the size and ossification of growing deer, we considered only young animals of each sex for which the metacarpus was not completely fused (stages 1 and 2). The two periods considered were: the winter of 1993 for animals born in very high density (92 individuals/km^2) and the combination of the winters of 1994 and 1995 for animals born in lower density (23 individuals/km^2). The effect of density on the total length of metacarpus was analysed for each sex by means of general lineal models (GLM), one-way ANCOVA. In this analysis, the covariable was age and the treatment was animal density (high density *versus*