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The ontogeny of bone growth in two species of dormice: Reconstructing life history traits

Ontogénie de la croissance osseuse chez deux espèces de dormice

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ABSTRACT

Though bone histology has become a powerful tool to reconstruct life history strategies and physiology in living and extinct reptiles and amphibians, it is of limited use in mammals. Dormice (Myoxidae) are good candidates for assessing the relation between bone microstructure and life history due to their long life span, marked physiological cycles and negligible bone remodelling. We carried out the most comprehensive study so far analyzing 16 wild individuals of unknown age belonging to two different species of dormice, *Glis glis* and *Eliomys quercinus*. Our study shows a high degree of consistency in the number of resting lines present in bones of the same individual, with femora providing the most accurate age estimations. Moreover, the presence of a single LAG in some juveniles allows discerning between offspring from different reproductive events (early or late litters).

RÉSUMÉ

Bien que l'histologie des os soit devenue un outil précieux pour la reconstitution des stratégies de l'histoire de la vie et de la physiologie chez les reptiles et amphibiens vivants et éteints, elle est d'une utilité limitée chez les mammifères. Les Dormice (Myoxidae) sont de bons candidats pour évaluer la relation entre microstructure de l'os et histoire de la vie, en raison de leur longue durée de vie, de leurs cycles physiologiques marqués et des modifications négligeables de leurs os. Nous avons réalisé l'étude jusqu'à présent la plus complète, en analysant 16 individus sauvages d'âge inconnu, appartenant à deux différentes espèces de dormice, *Glis glis* et *Eliomys quercinus*. Notre étude montre un degré élevé de cohérence dans le nombre de lignes de repos présentes dans les os du même individu, avec les fémurs fournissant les estimations d'âge les plus précises. En outre, la présence d'un unique LAG chez certains juvéniles permet de faire la distinction entre progénitures, à partir de différents évènements de la reproduction (portées récentes ou anciennes).

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1. Introduction

Life history is the schedule of events in the life of an organism from conception to death, with growth rate, age at first reproduction and length of reproductive span (generally equalling longevity) being of special importance because of their direct impact on fitness (Ricklefs, 2007). Life histories are strategies to enhance reproductive success by adjusting the developmental schedule to current environmental conditions. The study of life histories, hence, provides valuable insights into ecological conditions, biodiversity, demography, vulnerability and many other aspects of a species' biology and ecology (Ricklefs, 2007; Roff, 2002; Stearns, 1992). Therefore, an understanding of life history strategies is key to conservation management of endangered species. Even more, reconstruction of life histories from the past in their environmental context provides important cues to reconstruct past ecosystem dynamics or to predict the vulnerability and survival chance of extant populations (Köhler and Moyà-Solà, 2009; Raia and Meiri, 2006; Raia et al., 2003; Schwartz et al., 2002).

Bones and teeth of vertebrates record important events that took place during development (Klevezal, 1996), amongst them two important life history traits: the transition from young to adult (age at first reproduction, also called the age at sexual maturity) and age at death (which in some cases coincides with maximum longevity). One important goal of hard tissue histology is to estimate these life history components in extant and fossil vertebrates (Jordana and Köhler, 2011; Köhler, 2010; Köhler and Moyà-Solà, 2009).

The biological concept of "adult" is undeniably the attainment of sexual maturity, which is not to be confounded with somatic maturity. Sexual maturity can be attained before somatic maturity (in *Homo* for instance) or after (for instance in birds, Erickson et al., 2007). Bone tissue records age at sexual maturity in form of an important decrease in the rate of periosteal bone apposition (Chinsamy-Turan, 2005; Klevezal, 1996). This has a biological explanation based on the concept of trade-offs in life history theory. Because energy is limited, resources must be shared between different vital functions. As long as an organism needs to grow in order to attain a minimum size for successful reproduction, resources are channelled towards growth (and maintenance). As soon as this size is attained, resources are channelled away from growth towards reproduction (Ricklefs, 2007; Roff, 2002; Stearns, 1992). In mammalian bone, this is usually recorded as the transition from fast-growing to slow-growing tissue or even to a halt in bone apposition. It is a common believe that in mammals, contrary to ectotherm vertebrates, bone growth stops completely. This, however, is not the case. Many mammals such as our myoxids, but also primates (Castanet et al., 2004; Klevezal, 1996), ungulates (Klevezal, 1996; Köhler and Moyà-Solà, 2009), bears and kangaroos (Chinsamy-Turan, 2005), and probably many others deposit various annual resting lines periosteally that indicate an alternation between ceasing and resuming growth. Such growth rings, or lines of arrested growth (LAGs) are characteristic features in bone tissues of ectotherms (reptiles and amphibians) (Guarino et al., 2003; Starck and Chinsamy, 2002; Tumarkin-Deratzian, 2007), but they have also been observed in endotherms (mammals and birds) (Castanet et al., 2004; Klevezal, 1996; Starck and Chinsamy, 2002). LAGs record cyclical cessation of bone growth and are deposited annually (Castanet et al., 2004; Chinsamy-Turan, 2005), except for certain amphibians, which form LAGs biannually in environments with a dry summer and a cold winter seasons (Chinsamy-Turan, 2005). The number of growth lines in histological cross sections, hence, provides the age of an individual, a fundamental trait for demographic studies such as reconstruction of growth curves (Stearns, 1992), determination of the age structure of populations (Guarino et al., 2003), and conservation management (Chinsamy and Valenzuela, 2008) among others. In mammals, where bone remodelling tends to increase with age, estimated ages must be considered as minimum ages (Castanet et al., 2004). The spatial organization of LAGs and the histology of tissue deposited during cycles of active osteogenesis result from both local and general rates and rhythms of bone growth (Castanet, 2006), and provide additional information about an organism's life history such as age at first reproduction, or environmental (especially resource) conditions.

Usually, studies of bone histology are conducted in vertebrates that grow continuously throughout their lives or at least over several years and that show little if any remodeling of their bone tissue such as living and extinct amphibians and reptiles including certain dinosaurs (Chinsamy-Turan, 2005; Chinsamy and Valenzuela, 2008; Erickson, 2005; Margerie de et al., 2002; Tumarkin-Deratzian, 2007), early birds (Cambra-Moo et al., 2006; Castanet et al., 2000) and mammal-like reptiles (Botha and Chinsamy, 2005; Bromage et al., 2009). Small mammals, in contrast, grow fast and reach somatic/sexual maturity long before their first year of life when the first LAG is deposited (Castanet et al., 2004). Therefore, their bone tissue is considered to provide little information about growth rates, age at maturity, age at death or other life history traits.

The common histological pattern of mammals is: (i) a bone matrix of highly vascularised reticular or plexiform type indicative of a high and constant rate of tissue deposition in juvenile individuals; (ii) rather abruptly followed by dense periosteal bone at the transition from juvenile to adult, indicative of an important decrease in growth rate. Later in life, rest lines can form in this periosteal region (Chinsamy-Turan, 2005). Mammals with an extended juvenile period, generally large mammals such as certain ungulates (Köhler and Moyà-Solà, 2009), follow a slightly different pattern with one or occasionally two LAGs deposited within the fast-growing bone tissue before the beginning of dense periosteal bone, indicating that the animal ceased and resumed relatively fast growth over two or three years before maturity. Some studies, however, provide compelling evidence that mammalian bone growth does not necessarily follow this apparently uniform pattern (Castanet, 2006; Castanet et al., 2004; Chinsamy and Hurum, 2006; Klevezal, 1996; Ponton et al., 2004). A recent example is the finding of reptile-like zonal bone in a