General palaeontology, systematics and evolution (Palaeoecology)

Tracing the evolution of fitness components in fossil bovids under different selective regimes

Reconstitution de l'évolution des composants de la valeur sélective des bovidés fossiles sous différents régimes sélectifs

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ABSTRACT

Hard tissue histology is a valuable tool to reconstruct life history traits in fossil ungulates. We estimated certain fitness components (age at weaning, age at maturity, life span and generation time) in two fossil bovids that evolved under different selective regimes, the insular *Myotragus balearicus* and the continental *Gazella borbonica*. Our results provide evidence that the mainland *G. borbonica* conforms to the predictions for ungulates of similar body size. However, the insular *M. balearicus* does not fit predictions from body mass scaling, as it shows an important delay in age at weaning and, especially, in age at first reproduction. The considerable differences in the onset of these fitness components reflect the differences in resource availability and in extrinsic mortality that exist between insular and continental ecosystems. The significant delay in life history traits in *Myotragus* most likely resulted in severe constraints on the ability of this insular mammal to respond to ecological disturbances.

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RÉSUMÉ

L'histologie des tissus durs constitue un outil valable pour reconstituer les caractéristiques de l'histoire de la vie chez les ongulés fossiles. Nous estimons certaines composantes de la condition physique (âge au sevrage, âge à la maturité, espérance de vie, temps de vie d'une génération) chez deux bovidés fossiles qui évoluent sous deux différents régimes sélectifs, *Myotragus balearicus*, insulaire et *Gazella borbonica*, continental. Nos résultats montrent à l'évidence que *G. borbonica* vivant sur le continent est conforme aux prévisions relatives aux ongulés de la même taille. Toutefois, *M. balearicus,* au mode de vie insulaire, ne correspond pas aux prévisions quant à la graduation de la masse corporelle, car il montre un important retard pour l'âge de sevrage et plus particulièrement pour l'âge de la première reproduction.

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Les différences considérables dans la mise en place de ces composantes de valeur sélective reflètent les différences dans la disponibilité de ressources et dans la mortalité extrinsèque qui existent entre les écosystèmes insulaires et continentaux. Le retard significatif dans les caractéristiques de l'histoire de la vie chez *Myotragus* résulte vraisemblablement en sévères contraintes sur la capacité de ce mammifère insulaire à répondre aux perturbations écologiques.

1. Introduction

Life history strategies, the schedule of key events in an organism's lifetime, evolve in response to ecological conditions and have a direct bearing on fitness. Changes in the environment frequently trigger changes in life history traits that in turn shape demographic characteristics such as population growth rate, generation length, recruitment of juveniles, mortality rates and others. Therefore, analyses of life history traits are important at many levels and in many areas of biology and ecology (Brown and Sibly, 2006; Palkovacs, 2003; Ricklefs, 2007; Roff, 2002; Stearns, 1992).

A current omission in paleobiology is the reconstruction of life history traits in fossil mammals (Köhler and Moyà-Solà, 2009; Raia and Meiri, 2006; Raia et al., 2003; Schwartz et al., 2002). Analyses of life history traits in fossil species could provide important insights into biological and ecological aspects that cannot be studied in extant populations, such as long-term trends in population dynamics, evolution of fitness components under different selective regimes, causes underlying extinction, or impact of overhunting on fitness components (Jordana and Köhler, 2011; Köhler, 2010; Köhler and Moyà-Solà, 2009; Laurin, 2010; Ripple and Van Valkenburg, 2010).

Here we focus on the evolution of fitness components in fossil bovids that evolved under different selective regimes: (1) under the effect of limited food availability (insular environment, *Myotragus balearicus*); (2) under the effect of high extrinsic mortality (continental environment, *Gazella borbonica*), and compare our results with the knowledge about extant large herbivores.

M. balearicus is a Late Pleistocene dwarf bovid (Caprinae) endemic to the eastern Balearic Islands (Majorca and Minorca), which evolved under known selective pressures (chronically low resource levels and lack of predators) in a completely isolated ecosystem (Alcover et al., 1981; Köhler and Moyà-Solà, 2004, 2009; Moyà-Solà et al., 1999). *G. borbonica* is a small Pliocene bovid present at certain fossil bearing sites on the Iberian Peninsula (Kurtén, 2009).

1.1. Palaeohistology

Because physiological and life history strategies of extant and fossil vertebrates are recorded in their hard tissues, such as bone and teeth (Bromage et al., 2009; Chinsamy-Turan, 2005; Klevezal, 1996), paleohistology allows reconstruction of fitness components in extinct vertebrates. Life history traits are often associated with changes in the individual's energy budget, such as the channelization of resources away from growth toward reproduction (Ricklefs, 2007; Roff, 2002; Stearns, 1992).

These changes in the energy budget affect the rate of bone tissue apposition and leave marks on the growing bones, which allow reconstruction of certain life history traits (Castanet, 2006; de Margerie et al., 2002, de Margerie et al., 2004). Teeth provide additional information about life history strategies. Because mammalian dental tissue formation is periodic, cyclic variations during the ameloblast secretory activity lead to the formation of incremental marks in the enamel (Boyde et al., 1988). These allow determination of the rate and duration of dental growth and development, thus providing insight into developmental pathways and into life history traits of mammals (Beynon et al., 1998; Dean, 2006; Dean et al., 2001; Schwartz et al., 2002; Smith et al., 2007).

2. Material and methods

Because of the trade-off between growth and reproduction, mammals usually attain sexual maturity when final body size is reached. Therefore, the beginning of a dense outer circumferential layer (OCL) of organized lamellar tissue in the cortex of long bone shafts, formed when growth rate suddenly decreases, is considered as a proxy of the onset of fecundity (Chinsamy-Turan, 2005; de Margerie et al., 2002).

Estimate of age at sexual maturity in *M. balearicus* and in *G. borbonica* was based on counts of annual growth marks (lines of arrested growth 'LAGs') in transversal sections of long bone midshafts (skeletochronology, *see* Castanet, 2006; Castanet et al., 2004; Chinsamy-Turan, 2005; Erickson, 2005).

Fossil material: We sectioned 60 femora of *M. balearicus* from four sites (Cova de Llenaire, Es Bufador, Cova de Moleta and Son Maiol). The sample comprises all ages, from neonate through very old individuals. Not all thin sections were sufficiently well preserved as to allow analysis of the microstructure, so that we used 18 well-preserved specimens that represent almost all ages. Material of *G. borbonica* comes from two Pliocene sites of Teruel (La Puebla de Valverde) and Soria (Layna), Spain. The sample comprises 21 long bones (humeri, femora, radius and tibiae) of different age stages: five juvenile individuals and 13 adult individuals. Three individuals lack their epiphyses, so that no information about their age was available from macroscopic observation. Our descriptions of bone tissues are based on the typological classification established by de Margerie et al., (2002).

In mammals, tooth eruption is an adaptive trait tightly associated with life history (Schultz, 1935, 1956; Smith, 2000). The eruption of first permanent molars is commonly associated with weaning (Franz-Odendaal et al., 2003;
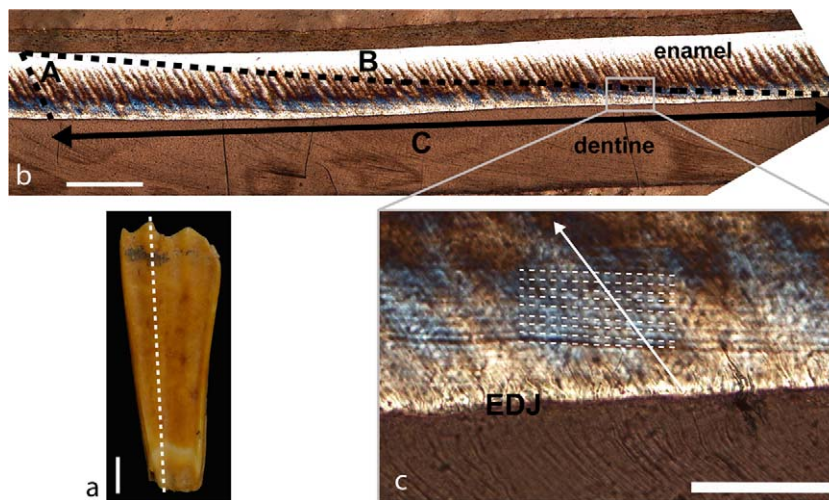
Fig. 1. Method used to calculate CFT in a first permanent lower molar of *M. balearicus* (MBCN 15801, Cova de Moleta, Majorca). (a) The first molar showing the cutting plane. Scale bar: 5 mm. (b) Detail of the histological section and technique used to calculate the increase in crown height as a function of time. Enamel prism (A), incremental feature (B), and increase in crown height during the complete path of an enamel prism from enamel–dentine junction to enamel surface (C). Occlusal region is on the right. Scale bar: 0.5 mm. (c) Fine incremental features in enamel (dotted lines) and enamel prism direction (arrow). EDJ: enamel-dentine junction. Scale bar: 0.1 mm.

Fig. 1. Méthode utilisée pour calculer CFT dans une première molaire inférieure permanente de *M. balearicus* (MBCN 15801, Cova de Moleta, Majorque). (a) Première molaire montrant le plan de coupe. Barre d'échelle : 5 mm ; (b) Détail de la section histologique et technique utilisée pour calculer l'accroissement de la hauteur de la couronne en fonction du temps. Prisme d'émail (A), trait incrémentiel (B) et accroissement de la hauteur de la couronne pendant l'évolution d'un prisme d'émail depuis la limite dentine-émail jusqu'à la surface de l'émail (C). Région occlusale sur la droite. Barre d'échelle : 0,5 mm. (c) Fins traits incrémentiels dans l'émail (lignes en pointillés) et direction du prisme d'émail (flèche). EDJ : limite dentine-émail. Barre d'échelle : 0,1 mm.

Macho, 2001; Macho and Williamson, 2002; Schwartz et al., 2002; Smith, 1989). We used first permanent lower molar (M_1) eruption time in *M. balearicus* as a proxy for age at weaning. M_1 eruption time in *M. balearicus* was estimated by calculating Crown Formation Time (CFT) in a slightly worn first lower molar (MBCN15801, Cova de Moleta, Majorca), using the incremental structures of enamel tissue (Beynon et al., 1998; Boyde, 1963; Bromage, 1991; Dean et al., 2001; Smith, 2008) observed in a thin section of the tooth cut longitudinally in the buccolingual plane at the mesial cusps (Fig. 1a). The method used to calculate CFT follows Jordana and Köhler (2011). Enamel prisms (Fig. 1b, A) mark the path of growth; incremental features (Fig. 1b, B) represent the position of the developing enamel front. Thus, the time required to form the distance comprised by the complete path of an incremental feature (Fig. 1b, C), is the same time required to form a prism from enamel-dentine junction to enamel surface (Fig. 1b, A). The latter is calculated by dividing the length of a prism by the average Daily Secretion Rate (DSR). DSR was calculated measuring the distance between adjacent fine incremental features (daily growth features) in different regions of the crown (Fig. 1c). Previously, this distance was compared along the inner and outer enamel and no significant differences were found. This process is repeated along the tooth crown in order to calculate the increase in crown height from cuspal region to cervical region as a function of time.

Additionally, we obtained X-ray images (Fig. 2) of an ontogenetic series of mandibles from *M. balearicus* (Cova de Moleta, Majorca), which allowed us to determine the extent of M_1 crown that is formed at the postnatal stage, since the formation of this molar already starts at the prenatal stage. Mandibles were scanned with a Siemens

Sensation 16 CT-scan at Hospital Mútua de Terrassa (Spain) with an interslice space of 0.2 mm. Images were analysed using the software OsiriX v.3.5.1.

The estimate of M_1 eruption time in *G. borbonica*, as a proxy for age at weaning, was not possible due to the lack of dental material.

Histological slides, both of bones and teeth, were made following standard procedures (Chinsamy-Turan, 2005; Klevezal, 1996) and examined under transmitted and polarized light. Specimens labeled ICP are housed at the Institut Català de Paleontologia, Universitat Autònoma de Barcelona, Bellaterra, Spain. Specimens labeled MBCN are housed at the Museu Balear de Ciències Naturals, Sóller, Majorca (Spain).

3. Results

3.1. Long bone histology of Gazella borbonica

Bone apposition and growth: Thin-sections from an ontogenetic series of long bones of *G. borbonica* reveal that the primary bone tissue consists of azonal bone. Juvenile specimens show fast growing fibrolamellar complex. The common vascularisation pattern is plexiform (Fig. 3a); however, occasionally reticular or longitudinal vascularisation is also observed (Fig. 3b). Adult specimens show a slow and residual growth, characterised by the presence of an OCL (Fig. 3c and Fig. 3d), with a maximum of two LAGs observed in an adult sample. Overall, the histological pattern found in *G. borbonica* is similar to the "common histological pattern" in mammals (Chinsamy-Turan, 2005), characterized by: (1) a high vascularisation in juveniles (reticular or plexiform types) without any interruptions in

Fig. 2. Radiologic study of an ontogenetic series of mandibles of *Myotragus balearicus*: (a) newborn individual (MBCN 12589), decidual premolars emerged but still unworn, a third of the first permanent molar crown is formed, but not emerged; (b) juvenile individual (MBCN 12592), decidual premolars emerged and worn, half of the first permanent molar is formed, but not emerged; (c) juvenile individual (MBCN 12593), decidual premolars considerably worn, first permanent molar erupted. Scale bar represents 20 mm.

Fig. 2. Étude radiologique d'une série ontogénique de mâchoire de *Myotragus balearicus* : (a) individu nouveau-né (MBCN 12589), prémolaires caduques, émergentes mais non encore usées, un tiers de la couronne de la première molaire permanente formée, mais non émergée ; (b) individu jeune (MBCN 12592), prémolaires caduques émergées et usées, moitié de la première molaire formée, mais non émergée ; (c) individu jeune (MBCN 12593), prémolaires caduques fortement usées, première molaire permanente sortie. Barre d'échelle = 20 mm.

growth rate, and (2) later in ontogeny, deposition of dense periosteal bone with rest lines (OCL).

Bone resorption and remodeling: Surprisingly, *G. borbonica* shows bone remodeling (dense Haversian Systems and endosteal bone), typical of adult individuals, already in juvenile specimens (Fig. 3b).

3.2. Long bone histology of Myotragus balearicus

Bone apposition and growth: Cross sections of neonates show fast growing fibrolamellar complex; the osteons are mostly circular (Fig. 4a). During the first year of life, the rate of bone deposition decreases and lamellar and/or parallel-fibered bone with primary osteons dominates (Fig. 4b). In some specimens, the rate of bone deposition decreases further before the formation of the first LAG (the cyclical cessation of bone apposition, presumably just after winter, Chinsamy-Turan, 2005), forming an annulus of lamellar nonvascular bone. The rest line is followed by another annulus (some individuals, Fig. 4c), or directly by lamellar bone with primary osteons, which form the zone before deposition of the second LAG. This pattern repeats from one LAG to the next (Fig. 4d), with some variations between individuals that regularly form a zone followed by an annulus before the next LAG and those that form lamellar bone with few primary osteons (zone), which is difficult or even impossible to distinguish from an annulus, before the next

LAG. Some individuals form simple LAGs, while others deposit up to 4 closely packed LAGs, presumably in a single event. The zones remain similar in width over several years of life (though there is some variation due to differential regional growth) and surprisingly similar between individuals, so that information that has been lost through remodeling or resorption in older specimens can be reconstructed from younger ones. When older than 8–10 years, many individuals decrease their inter-LAG distance or even form an OCL, though there is an important variability with many individuals being older but none younger than this threshold age. The oldest actively growing individual in our sample (Fig. 4e) is one of the largest specimens and it still has unfused epiphyses. Ten LAGs are evident in the compacta, but we estimated that 8 growth rings were obliterated during growth, thus making it approximately 18 years old.

Bone resorption and remodeling: Endosteal resorption starts as early as within the first year of life so that at deposition of the first LAG the neonate bone is almost completely removed. From approximately the second year onwards, cortical width remains more or less the same, which implies that bone removal is constant. At two years, the first Haversian systems develop in the inner cortex, and endosteal layers are deposited that increase with age. Haversian systems, however, remain rather scattered until an advanced age,
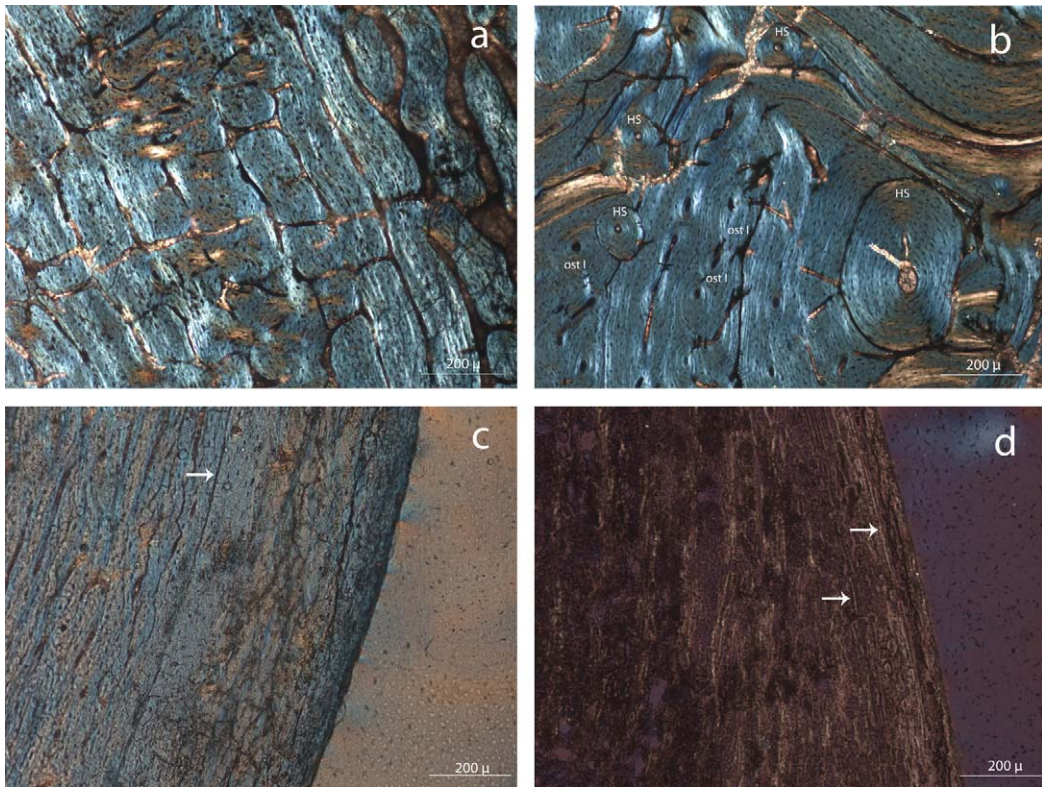
Fig. 3. Ontogenetic stages of *Gazella borbonica*. Micrographs of cortical sections of long bones shafts belonging to: (a) juvenile femur (ICP 44924) showing plexiform vascularisation; (b) juvenile tibia (ICP 26788-D) showing some longitudinal vascularisation (ost I) and secondary osteons (HS); (c) adult femora (ICP 28316) showing a LAG (arrow); (d) adult humerus (ICP 28315) showing two LAGs (arrows) at the OCL.
Fig. 3. Stades ontogéniques de *Gazella borbonica*. Microphotographies de sections corticales de charpente d'os longs appartenant à (a) un fémur de jeune (ICP 44924) montrant une vascularisation plexiforme ; (b) un tibia de jeune (ICP 26788-D) montrant une vascularisation longitudinale (ost I) et des ostéones secondaires (HS) ; (c) fémurs de jeunes (ICP 28316) montrant un LAG (flèche) ; (d) humérus d'adulte (ICP 28315) montrant deux LAGs au niveau de l'OCL.

and never invade the outermost region of the cortex.

3.3. M_1 eruption time in Myotragus balearicus

Following the technique illustrated in Fig. 1, we could calculate the increase in crown height from cuspal region to cervical region as a function of time in *M. balearicus* first permanent lower molar. Furthermore, the X-ray study of mandibles (Fig. 2) shows that one third of the final height of the M_1 crown is formed at the prenatal stage, and that three-quarters of its crown is already formed at emergence.

Putting histological and radiological studies together, we could estimate that M_1 CFT at neonatal stage is 0.2 year, at gingival emergence it is 0.8 years, and total CFT is 1.2 years. This indicates that in *M. balearicus*, M_1 was fully erupted at the age of one year, which is late compared to extant bovids where age at M_1 eruption ranges from 0.08 to 0.54 years (Smith, 2000). CFT in *Myotragus*, hence, strongly suggests a delayed age at weaning.

4. Discussion

Life history strategies are shaped by two factors, their scaling with body mass and their ecological context (resource availability, extrinsic mortality). Life history traits are fitness components because they regulate the balance between reproduction and growth and/or maintenance. They determine demographic characteristics such as population growth rate, generation time (the weighted mean age of mothers at offspring birth in a given population, Leslie, 1966), recruitment of juveniles, mortality rates, and others. Life history traits, hence, provide important insights into the ecology as well as into the vulnerability of species (Brown and Sibly, 2006; Calder, 1984; Palkovacs, 2003; Ricklefs, 2007; Roff, 2002; Stearns, 1992).

Ungulates are large mammals, which is reflected in most of their life history traits (Peters, 1983). They are characterized by low fecundity (only one or two offspring/year), a long potential life span, and strong iteroparity (Gaillard et al., 2000). Environmental variability and density-dependence, however, are documented to cause considerable phenotypic flexibility such as temporal variability in certain fitness components, which is especially obvious for age at sexual maturity (Gaillard et al., 2000; Saether, 1997). Age at maturity is a critical trait as it marks the moment in an individual's life at which resources are shifted away from growth toward reproduction (Kirkwood, 2005; Stearns, 1992). The age at first reproduction is found to provide reliable information about the ranking of a given species along the slow-fast continuum of life history traits (Gaillard et al., 2000). Among
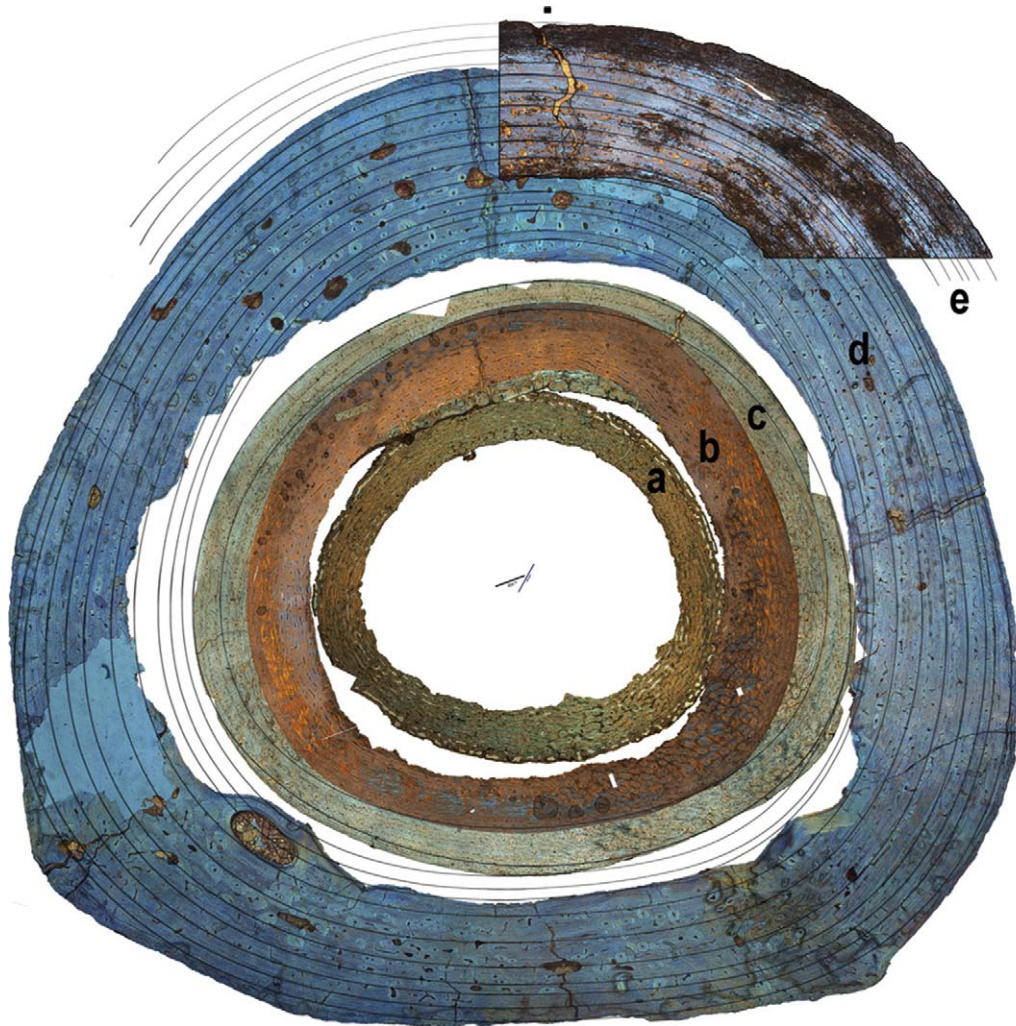
Fig. 4. Ontogenetic stages of *Myotragus balearicus*. Micrographs of cortical sections of femora with reconstructed lines of arrested growth (LAGs) from neonate through adult: (a) no LAG, neonate with fast growing fibrolamellar complex and mostly circular organized osteons (MBCN 6802, Cova de Moleta); (b) one LAG in the outer cortex, predominantly lamellar (parallel-fibred) bone with primary osteons (MBCN 6843b, Cova de Moleta); (c) two LAGs with annuli of lamellar non-vascular bone embedded in lamellar bone with primary osteons (MBCN 8989, Cova de Moleta); (d) 12 LAGs, no OCL, lamellar nonvascular bone alternating with lamellar bone with primary osteons, few haversian systems (ICP 26277, Es Bufador); (e) four further LAGs in a still actively growing individual without epiphyses (ICP 26321, Cova de Llenaire). Summing the lost LAGs, this individual reached an age of 18 years.

Fig. 4. Stades ontogéniques de *Myotragus balearicus*. Microphotographies de sections corticales de fémur avec des lignes reconstituées d'arrêt de croissance (LAGs) à partir du nouveau-né jusqu'à l'adulte : (a) pas de LAG, nouveau-né avec complexe fibrolamellaire croissant rapidement et ostéones pour la plupart organisés de manière circulaire (MBCN 6802, Cova de Moleta) ; (b) un LAG dans la partie externe du cortex, os à prédominance lamellaire (fibres parallèles) avec ostéones primaires (MBCN 6843b, Cova de Moleta) ; (c) deux LAGs avec anneaux d'os lamellaire non vascularisé insérés dans de l'os lamellaire à ostéones primaires (MBCN 8989, Cova de Moleta) ; (d) 12 LAGs, aucun OCL, os lamellaire non vascularisé alternant avec os lamellaire à ostéones primaires, quelques systèmes haversiens (ICP 26277, Es Bufador) ; (e) Quatre LAGs ultérieurs dans un individu en croissance active, sans épiphyses (ICP 26321, Cova de Llenaire). En additionnant les LAGs perdus, on trouve un âge de 18 ans pour cet individu.

populations, however, there is a certain degree of variability in this trait due to the dependence of female size and body condition on resource availability and population density, which may vary over time and geographic area. Thus, populations in habitats with low resource levels frequently show late primiparity (Gaillard et al., 2000; Saether, 1997). Age at first conception in females of *Gazella*, for instance, oscillates between 0.5 and two years (Mendelssohn et al., 1995; Nowak, 1999; Wronski and Sandouka, 2008), with *G. dorcas* from resource poor desert environments showing the broadest span and the

longest delay, from 190 days (Cassinello, 2005; Ralls et al., 1980) to 660 days (Furley, 1986; Yom-Tov et al., 1995). Despite these variations, ungulates are rather conservative in their life history strategies as summarized in their life history graph (Fig. 5), taken from Gaillard et al. (2000). In general terms, therefore, fitness components in ungulates are predictable.

Our results show that, indeed, our continental *G. borbonica* conforms to the predictions (Fig. 5). It is similar in size to *Gazella dorcas*, measured by the length of the radius (*G. borbonica* 132 mm, # ICP 28290, La Puebla
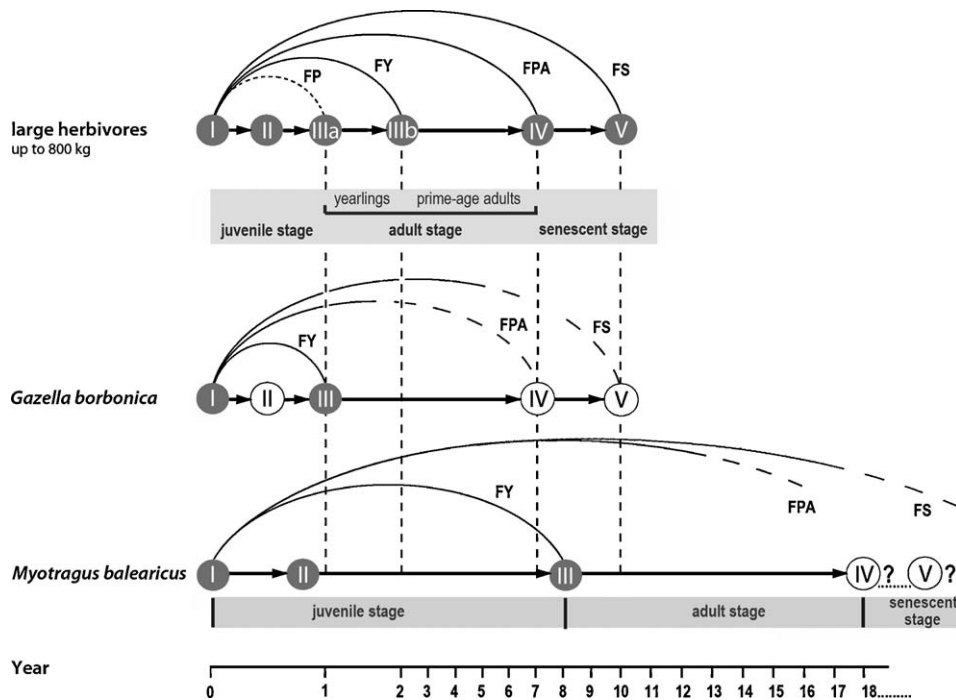
Fig. 5. Life cycle graph of large herbivore females (modified from Gaillard et al., 2000), and fossil *Gazella borbonica* and *Myotragus balearicus.* In our fossil species, it is impossible to distinguish between sexes. Nevertheless, because ungulate males are known to attain maturity later than females, long bones with the earliest appearance of OCL are classed as females. The conjecture that *G. borbonica* attained the senescent stage at around 7 years is based on the fitting of age at maturity with that expected from body mass scaling, and the similarity with other gazelles. Circled numbers schedule: I, birth; II, weaning; III, minimum age at primiparity; IV, prime aged; V, senescent. Grey circles: empirical; white circles: conjectural because of lack of data. Straight lines represent the transition from one age group to the next; curved lines describe reproduction: (FP) indicates fecundity of yearling females, given only in small to medium sized herbivores; (FY) indicates fecundity of young females (mostly 2-years-old), whereby in large species and in those living in resource poor environments or under nutritional stress primiparity is at 3–4 years; (FPA) indicates fecundity of prime-aged females; (FS) indicates fecundity of senescent females.

Fig. 5. Schéma du cycle de vie de femelles de grands herbivores (modifié selon Gaillard et al., 2000) et de *Gazella borbonica* et *Myotragus balearicus* fossiles. Dans nos espèces fossiles, il est impossible de faire la distinction entre les sexes. Néanmoins, comme les ongulés mâles sont connus pour atteindre leur maturité plus tard que les femelles, les os longs avec l'apparence la plus précoce sont classés en tant que femelles. La conjecture selon laquelle *G. borbonica* a atteint le stade sénescent autour de 7 ans est basée sur l'ajustement de l'âge à maturité avec celui attendu à partir de la graduation de la masse corporelle et la similitude avec les autres gazelles. Signification des nombres entourés d'un cercle : I, naissance ; II, sevrage ; III, âge minimum pour la mise bas ; IV, « force de l'âge » ; V, sénescence. Cercles gris : empirique ; cercles blancs : conjectural à cause du manque de données. Les lignes droites représentent la transition de l'un des groupes d'âge au suivant ; les lignes courbes décrivent la reproduction : (FP) indique la fécondité des femelles de l'année s'agissant seulement des herbivores de petite et moyenne tailles ; (FY) indique la fécondité des femelles jeunes (la plupart âgées de 2 ans), pour lesquelles chez les grandes espèces et celles vivant dans des environnements pauvres en ressources ou dans des conditions de stress nutritionnel, la primiparité se situe à 3–4 ans ; (FPA) indique la fécondité des femelles dans la force de l'âge, (FS) indique la fécondité des femelles sénescentes.

de Valverde; *G. dorcas*, 131.3 mm, # 7536 HH). Taking into account that *G. borbonica* is not an extreme desert form like some living species such as *Gazella dorcas* (Andrés and DeMiguel, 2008; Kurtén, 2009; Suc et al., 1995), it should be expected that *G. borbonica* reaches maturity well within the first year of life. Indeed, the first resting line appears in the OCL after overall growth has ceased.

M. balearicus, however, does not fit the predictions. The mean body mass (close to 25 kg at Cova de Moleta and Cova Estreta) (Köhler and Moyà, 2004) is comparable to that of *Gazella rufifrons*, which attains sexual maturity after 270 days (Walther, 1990), and smaller than that of the relative *Rupicapra rupicapra* (24–50 kg) which reaches maturity at two years (Nowak, 1999). Instead, growth decreased in *M. balearicus* at 8 years, at the earliest, indicating that it attained maturity at that age or later, with an important individual variability (Fig. 5). The high plasticity in this fitness component is likely related

to environmental variability and density dependence, factors found to commonly underlie variability in this trait in ungulates (Gaillard et al., 2000; Saether, 1997), and which are accentuated on small islands (MacArthur and Wilson, 1967).

Certain characteristics point to a correlated delay in at least two other fitness components, namely age at weaning and life span. Thus, the eruption of the first molar (M_1) in *M. balearicus* took place at the age of one year, contrasting with M_1 eruption in extant bovids, which ranges from 1 to 6 months (Smith, 2000). Owing to the straight correlation between M_1 eruption and weaning in mammals (Franz-Odendaal et al., 2003; Macho, 2001; Macho and Williamson, 2002; Schwartz et al., 2002; Smith, 1989), our results strongly suggest a delayed age at weaning for *M. balearicus*.

The large number of very old animals as seen in the extremely worn teeth housed in the many collections with
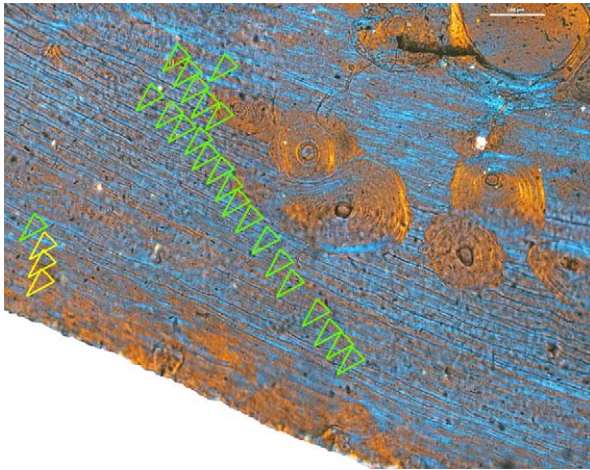
Fig. 6. The outer cortical layer (OCL) of an old individual with 26 LAGs. Green arrows show clearly visible LAGs, yellow arrows point to three further LAGs not visible in this section but in other regions of the slide.
Fig. 6. Partie externe du feuillet cortical (OCL) d'un vieil individu avec 26 LAG. Les flèches vertes montrent les LAG clairement visibles, les flèches jaunes pointent sur trois LAG ultérieurs non visibles sur cette section polie, mais visibles dans d'autres régions de la lame.

remains of *Myotragus*, is not known from any continental site. Bone histology also provides evidence that *Myotragus* reached surprisingly old ages for wild ungulates, as shown in Fig. 6. Moreover, in agreement with previous findings from living ruminants (Carranza et al., 2004; Veiberg et al., 2007), the outstanding increase in molar crown height (hypsodonty) in this species might not have evolved, at least not primarily, in response to diet but it rather increased the individual's life expectancy by extending the lifetime of the feeding apparatus. Altogether, this strongly suggests a high survival rate and an unusually long lifespan for this insular bovid (Köhler, 2010).

Contrary to our fossil continental gazelle, hence, the life history graph of the insular *M. balearicus* completely differs from the generalized graph for extant ungulates. It shows an important delay in all those fitness components that can be reconstructed.

Generation time is a fitness component with a great impact on population growth (Gaillard et al., 2000) and, hence, a key trait in the threat-rating system for long-lived and late-maturing organisms (Oates, 2006). We calculated generation time for *M. balearicus* using the equation by Pianka (2000):

$$T = (\alpha + \omega)/2$$

where *T* is generation time, α age at first reproduction, and ω age at last reproduction (here age of the oldest individual). This equation is only a very crude way to estimate *T*, and there are several problems involved in its use. Thus, for ungulate populations both the age at first reproduction and the age at last reproduction is available in a few exceptional cases only (for instance, Loison et al., 1999). Another source of error is the fact that senescence is pervasive among ungulates, with old females showing senescence in both survival and reproduction (Gaillard et al., 2000). The formula, however, calculates the midrange and, hence, does not take into account that the mean age of mothers

at offspring birth is skewed towards younger ewes. Generation time calculated with this equation, hence, must be expected to be higher than estimates obtained from field data. This is indeed the case when compared with data yielded by the allometric relationship between generation time and adult body mass in ungulates based on field observations: Ln (mean age of mother at time of birth) = 0.967 + 0.247 Ln (adult body mass) (Gaillard, 2007). Thus, the formula based on vital rates (age at first and last reproduction) provides an average generation time of 10 for ungulates of the size class of *Myotragus* (14–30 kg), while the body mass based formula yields an average generation time of only 5.6 for the same size class. Nevertheless, though generation time and other biological times correlate positively with body mass, there is an important variation even among populations (Gaillard, 2007) reflecting selection under different environmental conditions irrespectively of body mass (Veiberg et al., 2007). Thus, only the formula based on vital rates provides information about differences in generation times between species of comparable size. In a first attempt to estimate generation time in a fossil mammal, hence, we will use Pianka's formula to provide a rough idea of the ranking of *Myotragus* along the slow-fast continuum in life history traits.

The late onset of maturity and the outstanding longevity in *M. balearicus* provide the extraordinarily long generation time of approximately 17 years (based on an old individual with a minimum of 26 LAGs and assuming that it attained sexual maturity at a minimum age of 8 years; Fig. 6). Seventeen years is much longer than the average generation time of other bovids (Gaillard, 2007; Pianka, 2000) and is comparable only to estimates for long-lived and slow-maturing mammals such as large primates (Oates, 2006). A long generation time (K-species) makes sense in the context of resource limitation under insularity (MacArthur and Wilson, 1967). However, as in the case of primates, it makes the species vulnerable to those factors that increase mortality rate, such as predation pressure or hunting, because it imposes long time periods of recovery from declines in population size. We suggest that the long generation time of *M. balearicus* was the likely cause underlying its fast extinction after the arrival of man some 3000 years ago.

5. Conclusions

We analysed the evolution of fitness components in two fossil bovids under different selective regimes: the insular *M. balearicus* and the mainland *G. borbonica*. The former taxon evolved under chronic resource limitation and low extrinsic mortality, whereas the latter evolved under high extrinsic mortality. Results have been compared with those from studies of extant large herbivores. Ungulates are rather conservative in their life history strategies; however, environmental variability and density dependence are documented to cause important temporal variability in certain fitness components, which is especially obvious for age at sexual maturity. Our results show that *G. borbonica* conforms to the predictions for ungulates of similar body size; *M. balearicus*, however, completely differs from the generalized life cycle for extant ungulates, as it shows an important delay in all those fitness components that can be

reconstructed from the fossil remains, namely age at weaning, age at sexual maturity, life span and generation time. This variation in life history strategy makes sense in the context of resource limitation under insularity.

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