

Article

Sexual dimorphism across 3 stages of development in polygynous Artiodactyls is not affected by maternal care

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Abstract

In polygynous mammals, mature males are usually much heavier than females. Competition for females is intense, and few males reproduce. Given the importance of the male's body size for the reproduction and social life of these species, levels of sexual dimorphism were studied in 27 species of polygynous terrestrial cetartiodactyls at the 3 most significant stages of development: birth, 6 months of age, and adulthood. Overall, there were 3 different types of changes in male-to-female (M/F) mass ratios between birth and adulthood, corresponding to the 3 categories of adult dimorphism. The change in mass ratio between birth and 6 months of age was inversely correlated to the degree of dimorphism at birth. Most adult dimorphism was acquired after weaning. On the whole, postnatal maternal care seems to have no or even an inverse effect on the evolution of dimorphism, which is apparently not consistent with the assumption of greater maternal investment in male than in female offspring among polygynous mammals.

Key words: polygynous terrestrial cetartiodactyls, sexual dimorphism variations.

Polygyny occurs in many mammalian orders: Chiroptera and Rodentia (Clutton-Brock 1989; Bonatto et al. 2013), Lagomorpha (Rioja et al. 2008), Perissodactyla (Clutton-Brock 1989; Renan et al. 2015), Cetartiodactyla (Clutton-Brock 1989; Weckerly 1998), Carnivora (Kovacs and Lavigne 1986; Weckerly 1998; Lod  2001), and Primates (Harcourt et al. 1981; Clutton-Brock 1989; Leigh 1992, 1995; Weckerly 1998; Grueter and Van Schaik 2009). In polygynous mammals, mature males intensely compete for the control of females. In most species, they are heavier than females (Nowak 1999), although in a few species they are lighter (Ralls 1976). Dominant males are usually the heaviest ones (Dubost 1975; Townsend and Bailey 1981; McElligott et al. 2001; Jennings et al. 2010). Most often, the reproductive success of males increases with their body mass (Bergerud 1974; McElligott et al. 2001; Vanp  et al. 2010) and/or social rank (Wolff 1998; McElligott et al. 2001; DeYoung et al. 2006). Although breeding is not monopolised by one

or several males, as a rule, few of them reproduce (DeYoung et al. 2006).

Considering the importance of body characteristics of males in the reproductive and social life of the species, it appeared relevant to monitor the changes in sexual dimorphism during the growth process of young animals and to determine at which stage the dimorphism characteristic of each species was acquired. According to current knowledge, such a study had never been undertaken since most published data on sexual dimorphism have concerned neonates or adults, and rarely intermediate stages. Terrestrial cetartiodactyls are well-studied mammals, and most of them are polygynous and dimorphic to varying degrees. The first goal of this study was to assess dimorphism across their key stages of development. The second goal was to determine whether changes in dimorphism could be the result of maternal care. In accordance with the assumption of greater maternal investment in male than in female offspring in polygynous

mammals (Trivers and Willard 1973; Maynard Smith 1980), maternal care should be male-biased during the lactation period and have a positive effect on the development of sexual dimorphism. However, given the fact that young animals continue to grow long after maternal care ceases, much adult dimorphism could be acquired after weaning, without any direct maternal influence.

Materials and Methods

Previously published data and information that could be derived from growth curves were used, as well as some personal data. For both sexes of each species, data on body mass at definite stages, suckling time, age at the end of lactation, and the age at which individuals have attained their adult mass were retained. Three stages of individual development were assessed: birth, 6 months of age, and adulthood. Although maternal suckling rapidly diminished after birth, the age of 6 months corresponds to the full end of lactation in the species studied (mean weaning age: 5.08 ± 1.90 months), like in 80% of ungulates (Nowak 1999). This was, therefore, the most appropriate age for estimating the short-term results of maternal care. Furthermore, the animals reached 6 months before the onset of the harshest period of the year (winter) for temperate species. Only the species for which data were available for both sexes at every stage were retained. In total, 27 terrestrial cetartiodactyls were assessed from 6 families: Suidae (*Sus scrofa*), Tayassuidae (*Tayassu pecari*, *T. tajacu*), Tragulidae (*Hyemoschus aquaticus*), Cervidae (*Alces alces*, *Capreolus capreolus*, *Cervus canadensis*, *C. elaphus*, *Dama dama*, *Hydropotes inermis*, *Muntiacus reevesi*, *Odocoileus hemionus*, *O. virginianus*, *Rangifer tarandus*), Antilocapridae (*Antilocapra americana*), and Bovidae (*Aepyceros melampus*, *Antidorcas marsupialis*, *Bison bonasus*, *Commochaetes taurinus*, *Gazella thomsoni*, *Kobus leche*, *Ovis canadensis*, *Saiga tatarica*, *Sylvicapra grimmia*, *Syncerus caffer*, *Tragelaphus angasi*, *T. scriptus*).

The aim of this research was to study dimorphism variations. Since adult males of most species are heavier than females, the mass ratio of males to females was used as an index of sexual dimorphism. Thus, female mass was taken as the reference value for each species. When multiple data were available for the same species, the median was used. The retained species were grouped into 3 categories according to the distribution of adult mass ratios (see Figure 1).

Thus, 18 species with a high adult dimorphism (mass ratio > 1.2), 6 species with a low dimorphism (mass ratio between 1 and 1.2), and 3 species with no or an inverse dimorphism (mass ratio ≤ 1) have been distinguished.

Maternal care was distinguished from maternal investment since it concerned only the care afforded by the mother to her young during the postnatal phase. From the point of view of the young animals, the quantity and quality of milk ingested during the lactation period were evidently the most important factors to be considered, the other behaviors (sniffing, licking, playing, etc.) being essentially of a social nature. Therefore, the data available on total suckling time in 1 species with an inverse dimorphism, and in 9 other species with a high dimorphism were collected among the 27 species mentioned above. Suckling rate or the length of each suckling event was omitted, because it was considered as partial data. Because phylogeny could play a role in the results obtained, the relative closeness of taxa was estimated by the time of their divergence, according to Hassanin et al. (2012).

Distribution of mass ratios among age categories, as defined above, was tested with an analysis of variance F (Sokal and Rohlf 2001). Between 2 categories, comparisons were made with the Mann–Whitney U -test, since samples in each category did not permit parametric tests. For the data concerning all species, correlations were established using Pearson's r coefficient. Possible effects of phylogeny on the results were also studied at a specific level and at the family level, using the analysis of variance F .

Results

Mass ratio at the 3 main stages of development

Table 1 shows mass ratio values for the 27 species studied.

There was no correlation between adult mass ratio and female mass in all species ($r_{27}=0.230$, NS), as only in cervids or bovids ($r_{10}=0.234$ and $r_{12}=0.113$, respectively; NS). For example, adult dimorphism did not differ between species where female's mass was superior to 80 kg, those weighing 40–80 kg, and those weighing 20–40 kg ($U_{7,9}=24$, $U_{7,5}=10$, and $U_{9,5}=11$, respectively; NS), and the Rensch's rule occurring in other mammalian groups was not verified in polygynous artiodactyls.

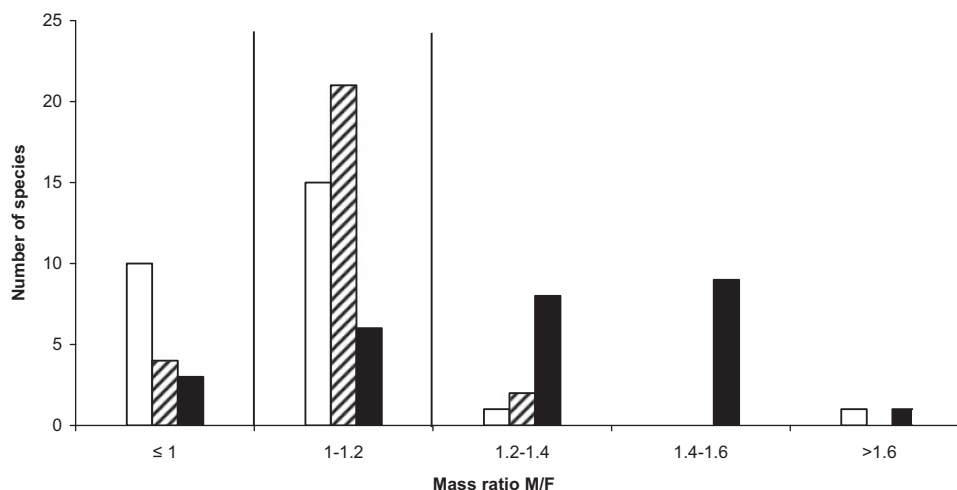


Figure 1. Distribution of mass ratios (M/F) in newborns (white bars), 6-month-old (dashed bars), and adults (black bars). The vertical lines indicate the 3 categories distinguished in this study.

Table 1. Mass ratio (M/F) at different stages of growth, median adult body mass, and ratio of time of M/F to attain the adult mass

Species	Mass ratio M/F		Median adult mass (kg)		Ratio of time M/F	Source
	Birth	6 months	Adult	Male		
Suidae						
<i>Sus scrofa</i>	1.000	1.019	1.495	91.1	61.0	Dubost et al. (2003); Gaillard et al. (1992); Orsi et al. (1992); Spitz et al. (1998)
Tayassuidae						
<i>Tayassu pecari</i>	0.909	0.917	1.088	36.0	33.1	Dubost et al. (2003)
<i>Tayassu tajacu</i>	0.839	1.000	1.209	22.0	18.2	Dubost et al. (2003)
Tragulidae						
<i>Hyemoschus aquaticus</i>	1.045	1.003	0.803	9.8	12.2	This study
Cervidae						
<i>Alces alces</i>	1.075	1.182	1.387	582.0	419.6	Bowyer et al. (2003); Franzmann et al. (1978); Franzmann and Schwartz (2007)
<i>Capreolus capreolus</i>	1.034	1.083	1.099	21.8	19.8	Andersen (1953); Klein and Strandgaard (1972); Pélabon et al. (1995); Wandeler and Huber (1969)
<i>Cervus canadensis</i>	1.182	1.072	1.331	319.5	240.0	Blood and Lovaas (1966); Byers and Moodie (1990); Dean et al. (1976); Pélabon et al. (1995)
<i>Cervus elaphus</i>	1.062	1.075	1.449	130.4	90.0	Byers and Moodie (1990); Clutton-Brock et al. (1981); Kelly et al. (1987); Mirchell et al. (1976); Pélabon et al. (1995); Radler (1979)
<i>Dama dama</i>	1.081	1.282	1.461	63.4	43.4	Birgersson (1998); Byers and Moodie (1990); Feldhamer et al. (1988); Pei (1996)
<i>Hydropotes inermis</i>	0.932	0.958	0.922	14.0	15.2	This study
<i>Muntiacus reevesi</i>	0.965	1.173	1.172	14.0	12.0	Chapman et al. (1997); Clutton-Brock et al. (1985); Pei (1996)
<i>Odocoileus hemionus</i>	1.078	1.118	1.469	94.4	64.3	Bandy et al. (1970); Byers and Moodie (1990); Mueller and Sadler (1980); Robinette et al. (1973); Weckerly (1998)
<i>Odocoileus virginianus</i>	1.057	1.163	1.584	84.7	53.5	Byers and Moodie (1990); Chesser and Smith (1987); Dubost et al. (2003); Pélabon et al. (1995); Weckerly (1998)
<i>Rangifer tarandus</i>	1.120	1.072	1.497	122.7	82.0	Krebs and McT. Cowan (1962); Lavigne and Barrette (1992); McEwan (1968); Nowak (1999); Pélabon et al. (1995); Weckerly (1998)
Antilocapridae						
<i>Antilocapra americana</i>	0.969	1.015	1.113	50.9	45.8	Byers (2003); Byers and Moodie (1990); Fairbanks (1993); Mirchell (1980)
Bovidae						
<i>Aepyceros melampus</i>	1.077	1.065	1.281	52.2	40.8	Anderson (1982); Dubost et al. (2003); Fairall and Braack (1976); Georgiadis (1985); Howells and Hanks (1975); Nowak (1999)
<i>Antidorcas marsupialis</i>	0.790	1.308	1.166	37.8	32.5	Cain et al. (2004); Dubost et al. (2003); Georgiadis (1985)
<i>Bison bonasus</i>	1.167	1.188	1.560	689.3	442.0	Krasnska and Krasinski (2002)
<i>Connochaetes taurinus</i>	1.283	1.067	1.270	240.0	189.0	Attrwell (1982); Dubost et al. (2003); Georgiadis (1985); Pélabon et al. (1995)
<i>Gazella thomsoni</i>	0.922	1.175	1.199	25.3	21.1	Dubost et al. (2003); Georgiadis (1985); Robinette and Archer (1971)
<i>Kobus leche</i>	0.597	0.898	1.310	97.0	74.0	Dubost et al. (2003); Georgiadis (1985)
<i>Ovis canadensis</i>	1.105	1.094	1.591	91.5	57.5	Festa-Bianchet et al. (1996); Hogg et al. (1992); Krausman and Bowyer (2003); Polak and Frynta (2009)
<i>Saiga tatarica</i>	1.129	1.088	1.392	40.4	29.0	Bannikov et al. (1967); Pélabon et al. (1995); Sokolov (1974)
<i>Sylvicapra grimmia</i>	0.919	1.141	0.963	16.1	16.7	Dubost et al. (2003); Georgiadis (1985); Wilson and Clarke (1962)
<i>Syncerus caffer</i>	0.732	0.914	1.296	688.0	531.0	Dubost et al. (2003); Georgiadis (1985)
<i>Tragelaphus angasi</i>	1.874	1.147	1.917	138.0	72.0	Georgiadis (1985)
<i>Tragelaphus scriptus</i>	1.049	1.139	1.530	45.1	29.5	Dubost et al. (2003); Georgiadis (1985); Simpson (1973)
Mean	1.037	1.087	1.317			

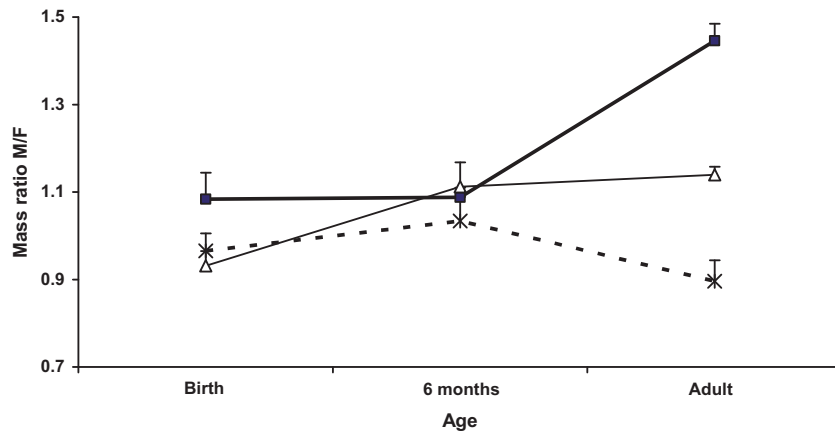


Figure 2. Mean (\pm SE) mass ratio M/F at birth, 6 months of age, and adulthood in highly dimorphic species (squares, bold line), weakly dimorphic species (triangles, thin line), and species with no or inverse dimorphism (crosses, dotted line).

The distribution of the 3 mass ratio categories as defined above differed between age groups ($P < 0.005$, $F_{2,78} = 15.33$; Figure 1). It was comparable at birth and at 6 months of age, but very different in adulthood. In highly dimorphic species, the mass ratio was higher in adults than in the 2 preceding stages ($P < 0.001$, $U = 3$ and $U = 20$, respectively; Figure 2). This was also the case in the weakly dimorphic species, although the difference was significant only with the mass ratio at birth ($P = 0.409$, $U = 16$, and $P = 0.001$, $U = 0$, respectively). On the contrary, in the species showing no or an inverse dimorphism, the adult mass ratio was slightly lower than those of the 2 preceding stages ($U = 1$ and $U = 3$, NS). At 6 months, the mass ratio was greater than at birth, but this was significant only in the weakly dimorphic species ($P < 0.05$, $U = 5$).

The absolute difference in mass ratios between adulthood and 6 months of age was greater than that between 6 months and birth in highly dimorphic species (0.358 ± 0.144 vs 0.134 ± 0.170 ; $P < 0.001$, $U = 29.5$), but not in the other 2 categories.

The first 2 ages did not reflect the 3 categories of dimorphism observed in adults. The mass ratio of newborns was higher in the highly dimorphic species than in the 2 other dimorphism categories ($P < 0.01$, $U_{6,18} = 18$, and $P \sim 0.05$, $U_{3,18} = 10$), but it did not differ between the latter 2 (0.93 ± 0.08 vs 0.97 ± 0.07 ; $P = 0.357$, $U_{3,6} = 7$). In contrast, the mass ratio at 6 months was comparable in the 3 categories: 1.09 ± 0.09 , 1.11 ± 0.14 , and 1.03 ± 0.10 , respectively ($U_{6,18} = 45$, $U_{3,18} = 18$, and $U_{3,6} = 5$; NS).

Changes in mass ratios between growth stages

There were 3 very different types of changes in mass ratios between birth and adulthood, according to the 3 categories of adult dimorphism (Figure 2). In highly dimorphic species, the mass ratio was comparable at birth and at 6 months of age, but considerably increased afterward until adulthood. On the contrary, in weakly dimorphic species the mass ratio significantly increased between birth and 6 months, and then very little until adulthood. Finally, in the species with no or an inverse dimorphism, the mass ratio increased slightly between birth and 6 months, and then decreased. Thus, the change in mass ratio from weaning to adulthood greatly differed from that occurring between birth and weaning.

Overall, between birth and 6 months of age, the mass ratio either increased or decreased according to the species, even in highly dimorphic ones (11 increases vs 7 decreases). Thus, its variation was inversely correlated to the value of mass ratio at birth ($P < 0.005$,

$r_{27} = -0.889$; Figure 3). This was also the case within each dimorphism category. The higher the mass ratio at birth was, the more it had decreased by 6 months. Inversely, low mass ratios at birth increased proportionally during the following 6 months. The relative mass of newborns (in percentage of the mother's mass) in species whose mass ratios increased from birth to 6 months of age did not differ from that in species whose mass ratios decreased ($9.22\% \pm 5.79\%$ vs $9.92 \pm 3.55\%$; $U_{8,19} = 64$, NS).

Globally, mass ratios were correlated between birth and adult stages ($P < 0.005$, $r_{27} = 0.575$), as in many mammals. This was not the case between mass ratios at 6 months of age and those at birth or adulthood ($r_{27} = 0.317$ and 0.321 , respectively; NS). However, these relationships were not verified in all dimorphism categories. Indeed, unlike highly dimorphic species, correlations between birth and adulthood were negative and not significant in the 2 lower dimorphism categories ($r = -0.388$ and -0.688 , respectively), as were those between birth and 6 months of age ($r = -0.506$ and -0.370 , respectively).

There was a high correlation between the adult mass ratio and the ratio of the time it took males to attain their adult mass relative to females ($P < 0.005$, $r_{24} = 0.657$; Figure 4). The adult mass ratio was high when growth was longer in males than in females, and on the contrary low or inverse when this growth was shorter. Thus, in the species with no or an inverse dimorphism, the mean ratio of time (M/F) to attain the adult mass was 0.841 ± 0.193 vs. 1.391 ± 0.172 in the weakly dimorphic species, and 1.671 ± 0.091 in the highly dimorphic species.

Concerning the relative closeness of taxa, there appeared to be no difference between the 3 categories of adult dimorphism ($F_{2,107} = 2.48$, NS). There was also no difference when non-ruminants, cervids and bovines were compared with each other ($F_{2,22} = 0.28$, NS).

Suckling time

Suckling time was significantly greater in male than in female fawns in only 2 highly dimorphic species, *C. canadensis* and *C. elaphus*. Nevertheless, the mass ratio (M/F) decreased by 9.3% from birth to 6 months of age in the former species, and increased by 1.2% in the second (Table 2). The same differences concerning the variations in mass ratios occurred in the other 8 species where the suckling time was comparable in both sexes (although it was sometimes slightly higher in males). Indeed, the mass ratio (M/F) varied from -4.3%

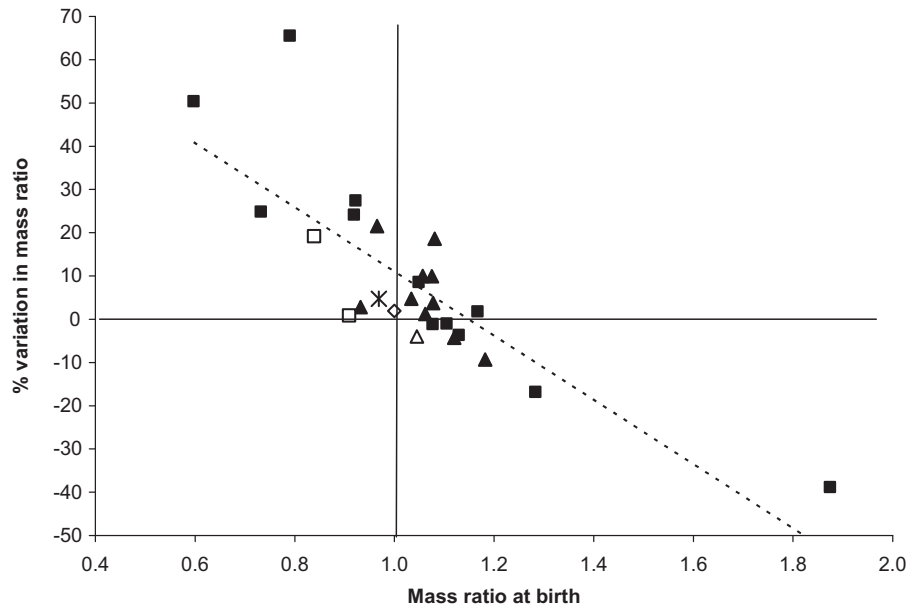


Figure 3. Variation (in %) of mass ratios (M/F) between birth and 6 months of age, according to their values at birth. Suidae: white diamond; Tayassuidae: white squares; Tragulidae: white triangle; Cervidae: black triangles; Antilocapridae: cross; Bovidae: black squares.

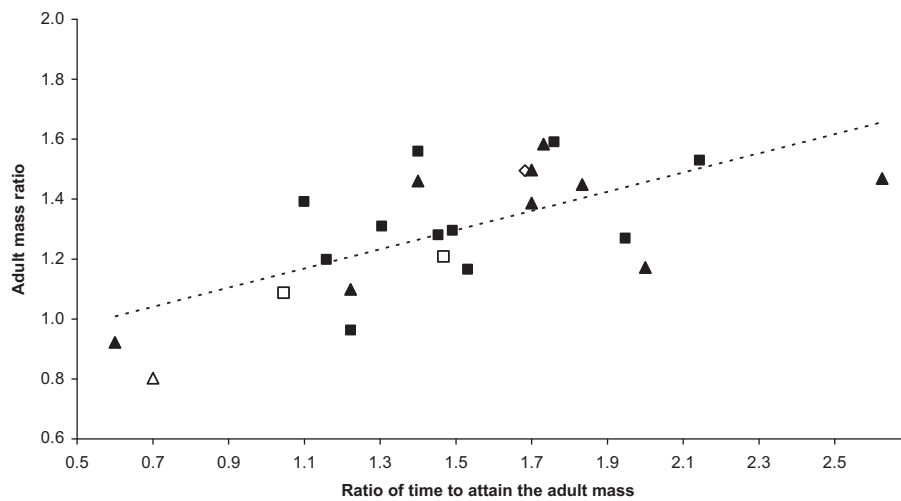


Figure 4. Adult mass ratio (M/F), according to the ratio of time of M/F to attain their adult mass. Suidae: white diamond; Tayassuidae: white squares; Tragulidae: white triangle; Cervidae: black triangles; Bovidae: black squares.

Table 2. Variation in mass ratio M/F and difference M/F in suckling time from birth to 6 months of age

Species	% Variation in mass ratio M/F	Suckling time M/F	Source
<i>B. bonasus</i>	1.8	~	Daleszczyk (2004)
<i>C. canadensis</i>	-9.31	>	Wengert and Kitchen (2008)
<i>C. elaphus</i>	1.22	>	Clutton-Brock et al. (1981); Landete-Castillejos et al. (2005)
<i>D. dama</i>	18.59	~	Gauthier and Barrette (1985); Birgersson and Ekvall (1997)
<i>H. inermis</i>	2.79	~	Mauget and Mauget (2009)
<i>O. hemionus</i>	3.71	~	Carl and Robbins (1988)
<i>O. virginianus</i>	10.03	~	Gauthier and Barrette (1985)
<i>O. canadensis</i>	-1.00	~	Hogg et al. (1992)
<i>R. tarandus</i>	-4.29	~	Lavigueur and Barrette (1992)
<i>T. tajacu</i>	19.19	~	Babbit and Packard (1990)

>: significantly superior in male than in female; ~: not different or not significantly superior in male than in female.

to +19.2% from birth to 6 months, according to the species. Therefore, no relationship could be established between the growth of young animals during the first 6 months of life and the suckling time of the mothers.

Discussion

In polygynous terrestrial cetartiodactyls, the distribution of mass ratios was globally comparable at birth and at 6 months of age, but very different in adults. This signifies that changes in mass ratios during the lactation period were, on the whole, of little importance.

As shown above, there were 3 different types of changes in mass ratios from birth to adulthood. Thus, there was no continuous increase in mass ratios from birth to adulthood, as could be expected, and the sexual dimorphism at 6 months appeared to be unrelated to the overall evolution of mass ratios. Except in weakly dimorphic species, this could mean that postnatal maternal care has little or no influence on adult sexual dimorphism.

The most significant outcome concerned the evolution of mass ratios between birth and 6 months of age. Depending on whether mass ratios were less than or greater than 1 at birth, they increased or decreased proportionally to their initial value during the following months. These variations could probably be explained by differences in the mass of newborns relative to their mothers. Indeed, Byers and Moodie (1990) suggested that the mother may invest more in male offspring than in female offspring only when the relative cost of the newborn is not too high. However, this was not the case among the species studied, in accordance with Pélabon et al. (1995). Thus, there was a sort of compensation in the development of young between the pre- and the postnatal periods, somewhat similar to that occurring between newborns of different weight. For example, individuals of twins or triplets were lighter at birth than single males or females in *O. virginianus* (Mueller and Sadler 1980), as in other species (Robinette et al. 1973; Mauget and Mauget 2009), but grew faster. The same could occur for the offspring of primiparous versus multiparous mothers (Robinette et al. 1973). This was apparently not the result of the mother's care, since the suckling time was not linked to the previous experience of mothers or to the number of young per litter (Gauthier and Barrette 1985; Byers and Moodie 1990).

In some species, the suckling time does not exactly correspond to the quantity of milk ingested (Hogg et al. 1992; Birgersson 1998; Cameron et al. 1999). This could be due to differences in sucking power between individuals or sexes, or in amount of milk immediately available. Thus, the more intense sucking behavior of male offspring could actually stimulate the mother to produce more milk (Lavigneur and Barrette 1992; Birgersson et al. 1998), as noted in *C. elaphus* (Landete-Castillejos et al. 2005). Furthermore, the total milk yield could be lower in primiparous than in multiparous females (Gauthier and Barrette 1985).

Males also could get more resources than females with a longer suckling period. In several pinnipeds, *Loxodonta africana*, *Equus caballus*, and *T. tajacu*, they were weaned a little later than females, although not significantly (Lee and Moss 1986; Babbit and Packard 1990; Lunn and Arnould 1997; Cameron and Lindaker 2000; Wilkinson and van Aarde 2001). There was no data available on other artiodactyls. However, it seems unlikely that this is also the case among them, since in many species daughters adopt home ranges overlapping those of their mothers, while sons disperse (Clutton-Brock et al. 1981).

It is also possible that the quality of milk is responsible for growth differences between sexes, as supposed by Birgersson and Ekvall (1997) and Birgersson (1998). Thus, in *C. elaphus*, mothers of sons produced greater yields of milk protein, fat, and lactose than mothers of daughters, and increased percentage of protein (Landete-Castillejos et al. 2005).

Growth differences during the period of maternal care could also be explained by differences in activity budget or foraging, as noted in some species (Byers and Moodie 1990; Hogg et al. 1992; Birgersson 1998). However, this was not the case in *Rangifer tarandus* and *Dama dama* (Lavigneur and Barrette 1992; Birgersson and Ekvall 1997; Birgersson et al. 1998).

Finally, the physiology has often been invoked to explain sexual growth differences (Lavigneur and Barrette 1992; Birgersson 1998; Hewison and Gaillard 1999). Thus, there could be a possibility that male fawns assimilate resources more efficiently, or allocate more resources to muscle and skeletal growth compared to females, and fewer resources to fat production which is more costly in energetic terms (Birgersson and Ekvall 1997; Birgersson et al. 1998). Presumably, testosterone could be responsible, probably because of its known anabolic properties, as noted by greater gain in biomass among intact compared to castrated male ungulates (Verme 1989; Smith and Leigh 1998).

However, whatever those reasons, they do not explain why mass ratios increased or decreased from birth to weaning inversely to their initial level among the species, and why they varied so much between weaning and adulthood after maternal care ceases. Since this phenomenon concerns only males, it did not appear in studies that take all young animals into account, regardless of their sex, such as those of Pélabon et al. (1995) and Andersen et al. (1998).

Except in weakly dimorphic species, the greatest mass change in males occurred after 6 months of age, which represents on average $90.9\% \pm 6.3\%$ ($n = 22$) of the total time from birth to adulthood in our species. Consequently, it appeared that mothers could not directly determine the capacity for males to obtain a high adult body mass, as expected in highly dimorphic species. In fact, as shown above, the final mass ratio was linked to the time it takes for each sex to attain adult mass, as already noted in mice and primates (Georgiadis 1985; Leigh 1992).

Apparently, these results do not concur with the assumptions of Trivers and Willard (1973) and Maynard Smith (1980). According to these authors, mothers are expected to preferentially invest in male offspring, the sex most capable of increasing their fitness. When male offspring are dominant, mothers can spread their genes more effectively through them than through female offspring, which differ less from other females in their reproductive capacities. Mothers could invest more in males than in females through several mechanisms, including a larger birth mass and a higher growth rate. Accordingly, it could be expected that this preference would have a positive effect on mass ratios during the lactation period, particularly in highly dimorphic species. This was not verified in this study. However, this does not exclude any role of mothers on the development of male offspring, as shown in *D. dama* (Birgersson et al. 1998).

There are very few data concerning mass ratio variations in the other polygynous mammals. In the primate *Papio sphinx*, there was no sexual difference in body mass at birth and at weaning age, contrary to adults where the mass ratio M/F reached the value of 3.43 (Smith and Leigh 1998; Setchell et al. 2001). Likewise, in 3 phocid species, the mass ratio M/F was low at birth (1.06–1.21), and it

remained stable or decreased from birth to weaning, contrary to the adult stage where it was much higher (1.60–4.24; Kovacs and Lavigne 1986). Thus, most sexual dimorphism was acquired after maternal care ceases in primates and carnivores, as in artiodactyls.

In conclusion, the mass ratio of polygynous artiodactyls increased or decreased between birth and weaning in the opposite direction to its value at birth. No relationship could be established between growth of young animals during the lactation period and total suckling time. Except in species showing no or an inverse dimorphism, the mass ratio was higher in adults than at birth or weaning stage. In reality, the adult mass ratio was highly correlated with the ratio of the time it took for males to attain their adult mass relative to females. Therefore, if individual mothers invest more in male than in female offspring in some species, at an interspecific level the mothers are not able to ensure a high level of dimorphism at weaning. Consequently, it is not possible to directly link the adult sexual dimorphism and the reproductive fitness of males with the maternal care, even in highly dimorphic species.

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