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ORIGINAL ARTICLE

Young and mature males have similar energy expenditure during the rut in a trophy-hunted population of Mediterranean mouflon

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Abstract

In polygynous ungulates, males invest time and energy to reproductive activities during the rut and this involvement is expected to increase with age due to different mating tactics in young versus adult males. In contrast, mating period is expected to be less costly for females for which late gestation and lactation are the most energetically demanding periods. However, empirical supports of these hypotheses through direct measures of reproductive effort are still limited in ungulate species, particularly in males. In addition, this general pattern may be modified in populations facing selective harvesting on adult males, where young males may experience less competition to mate and invest more energy during the rut. We investigated these hypotheses by studying the age- and sex-specific variations of kidney fat reserves from pre- to post-rut periods in a trophy-hunted population of Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.), a polygynous dimorphic mountain ungulate. Females were found to build up energy from the pre-rut to the post-rut periods, most likely to face with the subsequent costs of gestation/lactation that occur few months later. Conversely, kidney fat mass strongly decreased similarly in both young and mature males, and with the same magnitude, suggesting a strong investment of males of all ages in this population. This might be related to the selective hunting pressure on mature males this population is facing with. This result supports the need for more empirical and comparative studies to better grasp the influence of trophy hunting on reproductive effort in male ungulates.

Keywords Kidney fat · Reproduction cost · Rut · *Ovis gmelini musimon* × *Ovis* sp. · Ungulates

Introduction

In polygynous ungulate species, the reproductive success of females is generally highly dependent on their access to food resources, whereas males must rather compete to get access to females during the mating season (Emlen and Oring 1977). This sexual selection has favored fast growing males with a large body size in numerous ungulate species (Weckerly 1998), features that contrast with females, which invest in body condition and start to reproduce early at the expense of adult size (Andersson 1994; Clutton-Brock et al. 1988; Ralls 1977; Robert 1972). The timing of energy allocation to reproduction also differs between the sexes.

The period of highest energy expenditure for reproduction in females occurs during late gestation and lactation (Gittleman and Thompson 1988; Loudon 1985; Oftedal 1985). To sustain this high-energy demand, females in capital breeder species anticipate by building up energy as fat during the

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months prior to the energetically demanding period at late gestation and lactation (Clutton-Brock et al. 1989; Knopp et al. 1973).

On the contrary, males expend most energy for reproduction during the rutting season (Miquelle 1990; Yoccoz et al. 2002). During this period, different mating tactics are observed in male ungulates (Isvaran 2005), for example, the defense of females (harem) and territories containing resources in red deer (*Cervus elaphus*; Carranza et al. 1990); female-following and lekking behavior in fallow deer (*Dama dama*; Moore et al. 1995); and coursing and tending behaviors in wild goats and sheep (e.g., bighorn sheep *Ovis canadensis*; Hogg and Forbes 1997; mountain goats, *Oreamnos americanus*; Mainguy et al. 2008). These reproductive behaviors are highly energetically demanding for males, especially in most polygynous and dimorphic species (Garel et al. 2011; McElligott et al. 2003; Miquelle 1990; Yoccoz et al. 2002). In addition to the direct energy costs of such behaviors, polygynous males allocate most of their energy and time to reproductive behaviors during the rut with a depressed voluntary food intake and negative consequences on their body condition (Brivio et al. 2010; Clutton-Brock et al. 1982; Foley et al. 2018; Monteith et al. 2020; Mysterud et al. 2008; Pelletier et al. 2009). The investment of males in reproduction and the mating tactic they adopt generally also varies with age. Adult and larger males, with developed secondary sexual ornaments, are expected to be more attractive and to get greater access to females than younger males (Byers and Waits 2006). They also allocate more time and energy than immature males in intra-sex competition (e.g., fights) or tending (Clutton-Brock 1989; Clutton-Brock et al. 1992). By contrast, young males spend more time feeding and less time in costly reproductive behaviors and use alternative reproductive tactics (e.g., coursing; Bon et al. 1995; Mysterud et al. 2004; Pelletier et al. 2006; Willisch and Neuhaus 2009). As a consequence, the energetic investment for reproduction is expected to be lower in young males than in mature ones (Foley et al. 2018; Mysterud et al. 2004; Yoccoz et al. 2002), the former also balancing energy expenditure with growth and long-term reproductive success (Forsyth et al. 2005; Garel et al. 2011; Monteith et al. 2020).

This general pattern, however, has been challenged in populations of wild ungulates experiencing trophy hunting, with large-horned or large-antlered males being selectively targeted. In such populations, the biased hunting pressure against mature males may lead to a female-biased adult sex ratio and a higher proportion of young males compared with non-hunted populations. In the absence of adult males, young ones may then invest more energy in rutting activities and less energy in body growth, with potential short- and long-term consequences on their body mass, size, and survival (Bon et al. 1992; Garel et al. 2006; Mysterud 2014; Singer and Zeigenfuss 2002; Stringham and Bubenik 1975; but see Monteith et al. 2020 on yearling males of white-tailed deer *Odocoileus virginianus*).

To date, age-related variation in reproductive efforts in male ungulates has still received much less attention than in females. This discrepancy probably originates from the fact that reproductive investment in males results from multiple components (fighting, patrolling, tending, coursing; Mysterud et al. 2004) that are difficult to measure compared with the production of young in females (Clutton-Brock et al. 1989; Hewison and Gaillard 2001; Weladji et al. 2002). In addition, reproductive effort in male ungulates has often been studied from indirect measures, or with direct measures, such as changes in body mass (Mysterud et al. 2003, 2005), which are not always accurate proxies of energy expenditure (Garel et al. 2011). More studies are definitely required to better grasp the rutting ecology of ungulates (Mysterud et al. 2004).

Here, we aimed to contribute to this topic by investigating the energetic investments of females and of young and mature males during rutting activities in a population of sexually dimorphic Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.; Garel et al. 2007). In this capital breeder (Festa-Bianchet et al. 1998), most of the energy expended for reproduction relies on stored energy (Jönsson 1997; Stearns 1992). Variations in energy reserves, such as fat, are thus expected to reflect the costs of reproduction (Doughty and Shine 1997); hence, we used it to monitor energetic investment of mouflon during the rutting period (Garel et al. 2011; Riney 1955). We predicted that (H1) males should experience a much more marked decline in their fat reserves during rut than females. In addition, selective hunting of the largest horned males experienced by this population for several decades (Garel et al. 2007) has been related to an increasing participation of young males in rutting activities (Bon et al. 1995, 1992). We thus expected (H2) young males of our population to show a pattern of decline in fat reserve close to the one observed in adult males. By contrast, females are much less actively involved in mating activities in polygynous ungulates due to a short period of sexual receptivity. In addition, females do not stop feeding during the rut and are expected to build up energy that will be used a few months later to fulfill the high-energy requirements related to late gestation and lactation (Clutton-Brock et al. 1989; Knopp et al. 1973). As such, we expected females to increase their fat reserve during the mating period (H3), especially given the mild environmental conditions encountered in autumn–early winter in this population (Cransac et al. 1997).

Materials and methods

Study population and area

The studied population of Mediterranean mouflon inhabited the Caroux-Espinouse massif (43°38′N, 2°58′E, 17,000 ha, 150–1,124 m a.s.l.), in southern France. This area has a Mediterranean climate with both oceanic and mountainous influences (Baudière 1962), which often leads to the occurrence of summer droughts and to inconstant and fast melting snowfalls during winter, so that summer would be the most critical period for mouflon survival in this population (Garel et al. 2004).

Mediterranean mouflon is a dimorphic ungulate (sexual size dimorphism of 40.1%), with a mean spring-summer body mass (2002–2019 period) of 24.5 ± 4.1 kg (≥ 2 years old; $n = 683$) and 34.4 ± 5.5 kg (≥ 4 years old; $n = 222$) for adult females and adult males, respectively (Bourgoin et al. 2018; Garel et al. 2007). Sexual segregation occurs most of the year and is lowest during the rutting period (from October to early January with the most intense rutting activities from November to mid-December; Bon et al. 1993; Bourgoin et al. 2018). During rut, fights between males are common and males roam from one group of females to another. Although we expected interactions between males and the frequency of courtship behaviors to increase in sexually dimorphic species as males aged (Bon et al. 1995), this outcome did not occur in this population, where trophy hunting preferentially targeted males ≥ 6 years old (Garel et al. 2007) and led younger individuals (2.5–6.5 years old) to be involved in reproductive activities at similar levels to older individuals (Bon et al. 1992, 1995).

Data collection

We collected data from 89 sexually mature mouflon (29 females of ≥ 1.5 years old and 60 males of ≥ 2.5 years old; Garel et al. 2005a; Santiago-Moreno et al. 2000) legally harvested during the 2011–2012 hunting season (September 2011–February 2012). We assessed female age based on the number of permanent incisors, a reliable determination criterion until the age of 3.5 years (Rieck 1975). For males, we used counts of horn growth annuli (Geist 1966). We used the measure of the average kidney fat mass corrected by the average kidney mass (see below, Serrano et al. 2008) to investigate the energetic expenditure of mouflon during the rut. Indeed, fat is an energy-rich tissue that is mobilized when stored energy is required; thus, it should be among the most sensitive measures of energy investment (as compared for instance to mass changes; Garel et al. 2011). More specifically, we relied on kidney fat, which is known to be a reliable proxy of total body fat (Anderson et al. 1990; Caughley 1970; Riney 1955). To do so, we collected kidneys on harvested individuals and froze them at − 20 °C until analysis. In the laboratory, we first removed fat at both ends of each kidney and measured the mass (± 0.01 g) of the kidneys and the remaining fat around them (Riney 1955).

Statistical analyses

One old male (estimated age ≥ 11.5 years old) hunted mid-September was considered an outlier compared with other sampled animals, because it was in poor body condition and had no fat on its kidney. Thus, we removed this male from the dataset for the subsequent analyses. Based on the remaining animals for which we measured the two kidneys, we found no difference in the fat mass and kidney mass of the left and right kidneys (paired t tests: $t_{[81]} = -0.05$, $p = 0.964$ and $t_{[81]} = 1.75$, $p = 0.084$, respectively). We thus included animals with only data on one kidney ($n = 6/88$; 6.8%) in our analyses. For individuals with two kidneys, we computed the mean mass and fat mass from both kidneys.

We used linear models with the log-transformed fat mass as a response variable corrected by the log-transformed kidney mass to describe the body condition of mouflon (Garel et al. 2011; Serrano et al. 2008). Such analysis is recommended compared with the use of indices (e.g., the popular kidney fat index, Riney 1955), which are more susceptible to provide biased results when statistical assumptions, such as isometry or the absence of interaction among explaining factors (e.g., sex, age), are not met (Serrano et al. 2008). Other variables were the period (see below), sex (two levels: females and males), or a combined age class*sex factor (age_sex; three levels: females, young males and mature males; see below for information on young versus mature males) as well as the interaction between period and sex/age_sex factors. We considered the pre-rut (September–October), the rut (November–December), and the post-rut (January–February) periods (Bon et al. 1993). We pooled all females in a single age class—including only sexually mature individuals (≥ 1.5 years old; Garel et al. 2005a). It must be noted that restricting the analyses to multiparous females (≥ 2.5 years old, $n = 24$) by removing primiparous ones (1.5 years old, $n = 5$; Garel et al. 2005a) did not change our inferences. For males, full spermatogenesis (male puberty) occurred during their first year of life (Santiago-Moreno et al. 2000). However, physical maturity (asymptotic body growth being reached around 6 years old; Garel et al. 2005b; Hamel et al. 2016) would also contribute to successful mating in males (Bon et al. 1992, 1995; Lincoln 1998) and could be related to different reproductive tactics. Dominant adult males generally tended receptive females by following them and by impeding attempts to mate of other males. By contrast, young subordinates coursed females in an attempt to breach the defense of dominant males. We accounted for these behavioral differences in rutting activities among males by considering two age classes: young (2.5–4.5 years old, $n = 18$) versus physically mature males (≥ 5.5 years old; $n = 41$).

We ranked models based on the Akaike Information Criterion with second-order adjustment (AICc) to correct for small sample bias (Burnham and Anderson 2002). The models with the lowest AICc were considered to be the best models. We also computed Akaike weights (AICc weights) to compare the relative performance of models rather than only their absolute AICc value (Burnham and Anderson 2002). Weights can be interpreted as the probability that a model is the best one given the data and the set of candidate models. For comparisons of effect sizes, we considered non-overlapping 95% confidence intervals as statistically different and provided p values otherwise. We performed all the statistical analyses using R 3.6.1 (R Core Team, 2020).

Results

The best supported model included the interaction between sex and period but no age effect within males (Table 1). This model was six times more supported than the second-best model (AICc weights = 0.857 and 0.143, respectively) that included a difference in kidney fat between young and mature males (Appendix 1). All other models had no support (sum of their AICc weights close to 0; Table 1).

The best model supported sex-dependent kidney fat variation from the pre-rut to the post-rut period (H1 and H3 supported), and a similar level and pattern of variation of kidney fat for both young and mature males (Fig. 1; H2 supported). According to this model, the average fat mass in females was lowest during the pre-rut period [12.4 g $(8.3\text{–}18.4)_{95\%}$] and increased by 2–3 times during the rut [23.7 g $(14.4\text{–}38.8)_{95\%}$; $p = 0.035$] and the post-rut periods [36.5 g $(24.6\text{–}54.2)_{95\%}$; Fig. 1]. Conversely, in males, the average fat mass was maximum during the pre-rut period [42.9 g $(33.7\text{–}58.1)_{95\%}$] and strongly decreased during the rut [10.7 g $(8.3\text{–}13.8)_{95\%}$] and the post-rut periods [15.1 g $(11.1\text{–}20.7)_{95\%}$]. Compared with females, males had higher fat mass during the pre-rut period (3.5 times higher), but lower values during the rut and post-rut periods (Fig. 1).

Table 1 Selection of linear models based on corrected Akaike's Information Criterion (AICc) for testing the effects of the sex (females, males) or age_sex (females, young males, mature males) factors and of the period (pre-rut, rut, post-rut) on the fat mass of kidneys (log-transformed) from mouflon harvested in the Caroux-Espinouse massif, France, period 2011–2012

Model	AICc	ΔAICc	AICc weights
Sex + period + sex * period	177.9	0.0	0.857
Age_sex + period + age_sex * period	181.4	3.5	0.143
Period	212.5	34.6	0.000
Sex + period	214.4	36.5	0.000
Age_sex + period	216.6	38.7	0.000
Null	222.5	44.6	0.000
Sex	222.9	45.0	0.000
Age_sex	225.1	47.2	0.000

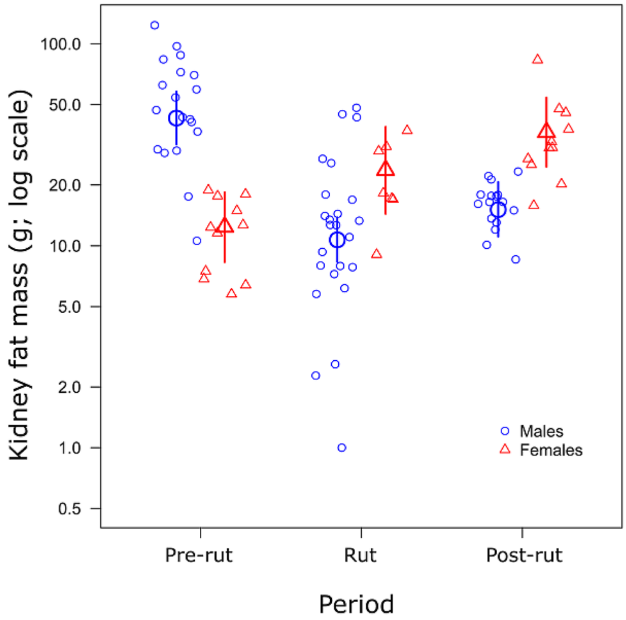

Fig. 1 Predicted values with 95% confidence intervals of mean kidney fat mass, and observed data, for female and male mouflon from the Caroux-Espinouse massif (southern France), for each period of 2 months during the September 2011—February 2012 period, based on the selected model (Table 1)

According to the second-best model, mature males would tend to have a better condition than young ones during the pre-rut period [53.5 g $(36.3;\ 79.0)_{95\%}$ and 32.2 g $(20.6;\ 50.4)_{95\%}$, respectively; $p = 0.083$; Appendix 1], while both categories had a similar condition during the rut [10.8 g $(7.9;\ 14.8)_{95\%}$ and 10.4 g $(6.7;\ 16.2)_{95\%}$, respectively; $p = 0.889$; during post-rut, only two young males were measured preventing us from statistical comparison].

Discussion

In agreement with our expectations (H1 and H3), the rutting period did not appear to be energetically demanding for females compared with males, for which fat mass markedly drops during that period, supporting the high energetic investment of males in rutting activities in this highly dimorphic species. We also observed a similar pattern of fat mass changes in young and mature males, results that also reveal a marked energetic investment of young males in rutting activities (in support of H2) in this population facing selective harvesting of old males (Garel et al. 2007).

In most capital breeder mammals, females build up energy as fat during the first two-thirds of gestation and then use this stored energy to support the high energetic costs associated with late gestation and lactation (Clutton-Brock et al. 1989; Knopp et al. 1973). Consistently, we found mouflon females increased their fat mass during the rutting period. We also recorded a higher fat mass in males compared with females before the rut, as previously observed with body mass or kidney fat in other ungulate species (e.g., Himalayan tahr *Hemitragus jemlahicus*: Forsyth et al. 2005; Cantabrian chamois *Rupicapra pyrenaica parva*: Pérez-Barbería et al. 1998; chamois *Rupicapra rupicapra*: Rughetti and Festa-Bianchet 2011). While females experience their highest energetic costs from the end of winter to summer (late gestation: March; lambing period: April–May; Bon et al. 1993), males—and especially mature males who do not invest energy in body growth, in contrast to young males—have lower energetic expenditure than females during those periods and are not constrained to trade-off between habitats offering the best food/cover conditions with the ones maximizing lamb survival, as do females (Marchand et al. 2014, 2015). In addition, the summer droughts that often occur in our study area, with observed consequences on behavior, body condition, and survival of mouflon (Bourgoin et al. 2011; Garel et al. 2004; Marchand et al. 2014), may not allow females to build up fat during summer, despite the fact that energetic costs of lactation decrease during this period. Accordingly, and as exemplified by our results, mature males can devote all their time to fully replenishing their fat reserves before entering the mating season (Appendix 1) compared with females, for which building an energy store was postponed during the rutting period. In addition, based on the observed increase of fat mass in female mouflon during the study period, we can assume that autumn–winter was not a limiting season for females in the Caroux-Espinouse (see also Garel et al. 2005a for demographic parameters).

During the rut, males experienced a marked decrease in their body condition (our results and e.g., Forsyth et al. 2005; Holand et al. 2006; Monteith et al. 2020; Rughetti and Festa-Bianchet 2011). These results support the hypothesis of a substantial cost of male reproduction in sexually dimorphic capital breeders that mostly rely on body energetic reserves. These costs result from the direct energy expenditure associated with rutting behaviors and from the reduced involvement in feeding activities (Bon et al. 1995; Brivio et al. 2010; Clutton-Brock et al. 1982; Monteith et al. 2020). Thus, costs may be higher than acquired energy and lead to a negative energetic balance and to the metabolism of their fat reserves during this period. The tendency for mature males to have a better condition compared with young ones before participating in rutting activities (second-best model; Appendix 1) may originate from a trade-off in the latter between accumulating body fat while still being in a period of intensive body growth (Hamel et al. 2016).

While reproductive investment in ungulate males increases with age (Clutton-Brock 1984; Clutton-Brock et al. 1982; Garel et al. 2011; Mysterud et al. 2004), we observed comparable energetic investments in both young and mature males. A high energetic investment of young males during rut has been previously observed in populations of wild ungulates experiencing trophy hunting, with large-horned or large-antlered males being selectively targeted. In such populations, the biased hunting pressure against mature, old males may lead to a female-biased adult sex ratio and a higher proportion of young males compared with non-hunted populations. Where there is a lack of mature males, young ones may then invest more energy in rutting activities and less so on body growth, with potential short- and long-term consequences on their body mass, size, and survival (Bon et al. 1992; Garel et al. 2006; Mysterud 2014; Singer and Zeigenfuss 2002). The studied population of mouflon also faced trophy hunting (Garel et al. 2007), offering opportunities for young individuals to be involved in reproductive activities at similar levels to mature individuals (see Bon et al. 1992, 1995). Such hunting pressure might have contributed to the high energetic investment of young males during the rut. However, further studies based on experimental design (e.g., Monteith et al. 2020) or on larger sample sizes comparing populations of mouflon facing high selective hunting pressures with non-hunted populations (acting as a control) would help to definitively support this hypothesis. The observed marked energetic investment of young males during the rut, while consistent with other knowledge on the influence of selective harvesting in this population (on horns size and shape; Garel et al. 2007), questioned the long-term consequences both in terms of survival and other fitness-related components (Festa-Bianchet et al. 2003; Forsyth et al. 2005; Garel et al. 2009; Singer and Zeigenfuss 2002; Stringham and Bubenik 1975). This result also supports the need for more empirical and comparative studies to better investigate the potential side effects of selective hunting on the rutting ecology of male ungulates (Milner et al. 2007).

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Author contributions GB: conceptualization, methodology, formal analysis, resources, data curation, writing—original draft, writing—review & editing, supervision, project administration, and funding acquisition. AL: formal analysis, investigation, and data curation. PM:

conceptualization, methodology, formal analysis, writing—original draft, and writing—review & editing. JD: resources and investigation. M-TP: resources and investigation. PM: resources and investigation. CI: resources and investigation. MG: conceptualization, methodology, formal analysis, resources, writing—original draft, writing—review & editing, project administration, and funding acquisition.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Code availability The code generated during the current study is available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflicts of interest On behalf of all authors, the corresponding author states that there is no conflict of interest. The authors declare that they have no conflict of interest.

Ethics approval All samples were collected from legally hunted mouflon. No animals were harvested only for the purpose of this study.

Consent to participate Not applicable.

Consent for publication Not applicable.

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