



HAL
open science

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

G. Bourgoïn, Alice Laurent, Pascal Marchand, Jeanne Duhayer, Marie-Thérèse Poirel, Patricia Michel, Christian Itty, Mathieu Garel

► To cite this version:

G. Bourgoïn, Alice Laurent, Pascal Marchand, Jeanne Duhayer, Marie-Thérèse Poirel, et al.. Young and mature males have similar energy expenditure during the rut in a trophy-hunted population of Mediterranean mouflon. *Mammalian Biology: Zeitschrift für Säugetierkunde*, 2021, 101 (1), pp.35 - 42. 10.1007/s42991-020-00084-0 . hal-03721733

HAL Id: hal-03721733

<https://vetagro-sup.hal.science/hal-03721733v1>

Submitted on 5 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 **Gilles BOURGOIN^{a,b,*}, Alice LAURENT^a, Pascal MARCHAND^c, Jeanne DUHAYER^{b,c},**
5 **Marie-Thérèse POIREL^{a,b}, Patricia MICHEL^d, Christian ITTY^c, Mathieu GAREL^c**

6

7 ^aUniversité de Lyon, VetAgro Sup - Campus Vétérinaire de Lyon, Laboratoire de parasitologie
8 vétérinaire, 1 avenue Bourgelat, BP 83, F-69280 Marcy l'Etoile, France.

9 ^bUniversité de Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Evolutive
10 UMR 5558, F-69622 Villeurbanne, France.

11 ^cOffice Français de la Biodiversité, Unité Ongulés Sauvages, 5 allée de Bethléem, Z.I. Mayencin, F-
12 38610 Gières France.

13 ^dGroupement d'Intérêt Environnemental et Cynégétique du Caroux-Espinouse, Fagairolles F-34610,
14 Castanet-le-Haut, France

15

16

17 ***Corresponding author:**

18 G. Bourgoïn, VetAgro Sup, Laboratoire de parasitologie, 1 avenue Bourgelat, BP 83, F-69280
19 Marcy l'Etoile, France.

20 E-mail address: gilles.bourgoïn@vetagro-sup.fr

21 Telephone: +33 (0)4 78 87 27 63

22 ORCID: 0000-0003-0993-0741

23

24 Short title: Energy expenditure during the rut in Mediterranean mouflon

25 **Abstract**

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

43 **Keywords:**

44 Kidney fat; reproduction cost; rut; *Ovis gmelini musimon* × *Ovis* sp.; ungulates

45 **Declarations**

46 **Funding:** the study was financially supported by VetAgro Sup, LBBE and ONCFS.

47 **Conflicts of interest/Competing interests:** On behalf of all authors, the corresponding author
48 states that there is no conflict of interest.

49 **Ethics approval:** All samples were collected from legally hunted mouflon. No animals were har-
50 vested only for the purpose of this study.

51 **Consent to participate:** Not applicable

52 **Consent for publication:** Not applicable

53 **Availability of data and material:** The datasets generated during the current study are available
54 from the corresponding author on reasonable request.

55 **Code availability:** The code generated during the current study are available from the correspond-
56 ing author on reasonable request.

57 **Authors' contributions:**

58 **Gilles Bourgoïn:** Conceptualization, Methodology, Formal analysis, Resources, Data Curation,
59 Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding
60 acquisition.

61 **Alice Laurent:** Formal analysis, Investigation, Data Curation.

62 **Pascal Marchand:** Conceptualization, Methodology, Formal analysis, Writing - Original Draft,
63 Writing - Review & Editing.

64 **Jeanne Duhayer:** Resources, Investigation.

65 **Marie-Thérèse Poirel:** Resources, Investigation.

66 **Patricia Michel:** Resources, Investigation.

67 **Christian Itty:** Resources, Investigation.

- 68 **Mathieu Garel:** Conceptualization, Methodology, Formal analysis, Resources, Writing - Original
- 69 Draft, Writing - Review & Editing, Project administration, Funding acquisition.

70 **1. Introduction**

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

78 The period of highest energy expenditure for reproduction in females occurs during late gestation
79 and lactation (Gittleman and Thompson, 1988; Loudon, 1985; Oftedal, 1985). To sustain this high
80 energy demand, females in most species anticipate by building up energy as fat during the months
81 prior to the energetically demanding period at late gestation and lactation (Clutton-Brock et al.,
82 1989; Knopp et al., 1973).

83 On the contrary, males expend most energy for reproduction during the rutting season (Miquelle,
84 1990; Yoccoz et al., 2002). During this period, different mating tactics are observed in males
85 ungulates (Isvaran, 2005), for example, the defense of females (harem) and territories containing
86 resources in red deer (*Cervus elaphus*; Carranza et al., 1990); female-following and lekking
87 behavior in fallow deer (*Dama dama*; Moore et al., 1995); and coursing and tending behaviors in
88 wild goats and sheep (e.g., bighorn sheep *Ovis canadensis*; Hogg and Forbes, 1997; mountain goats,
89 *Oreamnos americanus*; Mainguy et al., 2008). These reproductive behaviors are highly
90 energetically demanding for males, especially in most polygynous and dimorphic species (Garel et
91 al., 2011; McElligott et al., 2003; Miquelle, 1990; Yoccoz et al., 2002). In addition to the direct
92 energy costs of such behaviors, polygynous males allocate most of their energy and time to
93 reproductive behaviors during the rut with a depressed voluntary food intake and negative
94 consequences on their body condition (Brivio et al., 2010; Clutton-Brock et al., 1982; Foley et al.,
95 2018; Monteith et al., 2020; Mysterud et al., 2008; Pelletier et al., 2009). The investment of males

96 in reproduction and the mating tactic they adopt generally also varies with age. Adult males invest
97 in developing secondary sexual traits, such as horns or antlers, to be more attractive and to get
98 greater access to females than younger males (Byers and Waits, 2006). They also allocate more
99 time and energy than immature males in intra-sex competition (e.g., fights) or tending (Clutton-
100 Brock, 1989; Clutton-Brock et al., 1992). By contrast, young males spend more time feeding and
101 less time in costly reproductive behaviors and use alternative reproductive tactics (e.g., coursing;
102 Bon et al., 1995; Mysterud et al., 2004; Pelletier et al., 2006; Willis and Neuhaus, 2009). As a
103 consequence, the energetic investment for reproduction is expected to be lower in young males than
104 in mature ones (Foley et al., 2018; Mysterud et al., 2004; Yoccoz et al., 2002), the former also
105 balancing energy expenditure with growth and long-term reproductive success (Forsyth et al., 2005;
106 Garel et al., 2011; Monteith et al., 2020).

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

116 To date, age-related variations in reproductive efforts in male ungulates has still received much less
117 attention than in females. This discrepancy probably originates from the fact that reproductive
118 investment in males results from multiple components (fighting, patrolling, tending, coursing;
119 Mysterud et al., 2004) that are difficult to measure compared with the production of young in
120 females (Clutton-Brock et al., 1989; Hewison and Gaillard, 2001; Weladji et al., 2002). In addition,
121 reproductive effort in male ungulates has often been studied from indirect measures, or with direct

122 measures, such as changes in body mass (Mysterud et al., 2005, 2003), that are not always accurate
123 proxies of energy expenditure (Garel et al., 2011). More studies are definitely required to better
124 grasp the rutting ecology of ungulates (Mysterud et al., 2004).

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

141 As such, we expected females to increase their fat reserve during the mating period (H3), especially
142 given the mild environmental conditions encountered in autumn–early winter in this population
143 (Cransac et al., 1997).

144

145

146

147

148 **2. Material and methods**

149 **2.1. Study population and area**

150 The studied population of Mediterranean mouflon inhabited the Caroux-Espinouse massif
151 (43°38'N, 2°58'E, 17,000 ha, 150-1,124 m a.s.l.), in southern France. This area has a Mediterranean
152 climate with both oceanic and mountainous influences (Baudière, 1962), which often leads to the
153 occurrence of summer droughts and to inconstant and fast melting snowfalls during winter, so that
154 summer would be the most critical period for mouflon survival in this population (Garel et al.,
155 2004).

156 Mediterranean mouflon is a dimorphic ungulate (sexual size dimorphism of 40.1%), with a mean
157 body mass (2002-2019 period) of 24.5 ± 4.1 kg (≥ 2 years old; $n = 683$) and 34.4 ± 5.5 kg (≥ 4 years
158 old; $n = 222$) for adult females and adult males, respectively (Bourgoin et al., 2018; sexual size
159 dimorphism of 66%; Garel et al., 2007). Sexual segregation occurs most of the year and is lowest
160 during the rutting period (from October to early January with the most intense rutting activities
161 from November to mid-December; Bon et al., 1993; Bourgoin et al., 2018). During rut, fights
162 between males are common and males roam from one group of females to another. Although we
163 expected interactions between males and the frequency of courtship behaviors to increase in
164 sexually dimorphic species as males aged (Bon et al., 1995), this outcome did not occur in this
165 population, where trophy hunting has decreased the proportion of old males (average age of hunted
166 males = 10.2 years, in 1996-2002; Garel et al., 2007) and led young individuals (2.5-6.5 years old)
167 to be involved in reproductive activities at similar levels as mature individuals (Bon et al., 1995,
168 1992).

169 **2.2. Data collection**

170 We collected data from 89 sexually mature mouflon (Garel et al., 2005a; 29 females (≥ 1.5 years
171 old) and 60 males (≥ 2.5 years old); Santiago-Moreno et al., 2000) legally harvested during the
172 2011–2012 hunting season (September 2011–February 2012). We assessed female ages based on

173 the number of permanent incisors, a reliable determination criterion until the age of 3.5 years
174 (Rieck, 1975). For males, we used counts of horn growth annuli (Geist, 1966). We used the measure
175 of the average kidney fat mass corrected by the average kidney mass (see below, Serrano et al.,
176 2008) to investigate the energetic expenditure of mouflon during the rut. Indeed, fat is an energy-
177 rich tissue that is mobilized when stored energy is required; thus, it should be among the most
178 sensitive measures of energy investment (as compared for instance to mass changes; Garel et al.,
179 2011). More specifically, we relied on kidney fat, which is known to be a reliable proxy of total
180 body fat (Anderson, 1981; Caughley, 1970; Riney, 1955). To do so, we collected kidneys on
181 harvested individuals and froze them at -20°C until analysis. In the laboratory, we first removed fat
182 at both ends of each kidney and measured the mass (± 0.01 g) of the kidneys and the remaining fat
183 around them (Riney, 1955).

184 **2.3. Statistical analyses**

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

193 We used linear models with the log-transformed fat mass as a response variable corrected by the
194 log-transformed kidney mass to describe the body condition of mouflon (Garel et al., 2011; Serrano
195 et al., 2008). Such analysis is recommended compared with the use of indices (e.g., the popular
196 kidney fat index, Riney, 1955), which are more susceptible to provide biased results when statistical
197 assumptions, such as isometry or the absence of interaction among explaining factors (e.g., sex,
198 age), are not met (Serrano et al., 2008). Other variables were the period (see below), sex (two

199 levels: females and males), or a combined age class*sex factor (*age_sex*; three levels: females,
200 young males and mature males; see below for information on young versus mature males) as well as
201 the interaction between period and sex/*age_sex* factors. We considered the pre-rut (September-
202 October), the rut (November-December), and the post-rut (January-February) periods (Bon et al.,
203 1993). We pooled all females in a single age class—including only sexually mature individuals (\geq
204 1.5 years old; Garel et al., 2005a). It must be noted that restricting the analyses to multiparous
205 females (≥ 3.5 years old, $n = 24$) by removing primiparous ones (1.5 years old, $n = 5$; Garel et al.,
206 2005a) did not change our inferences. For males, full spermatogenesis (male puberty) occurred
207 during their first year of life (Santiago-Moreno et al., 2000). However, physical maturity
208 (asymptotic body growth being reached around 6 years old; Garel et al., 2005b; Hamel et al., 2016)
209 would also contribute to successful mating in males (Bon et al., 1995, 1992; Lincoln, 1998) and
210 could be related to different reproductive tactics. Dominant adult males generally tended receptive
211 females by following them and by impeding attempts to mate of other males. By contrast, young
212 subordinates coursed females in an attempt to breach the defense of dominant males. We accounted
213 for these behavioral differences in rutting activities among males by considering two age classes:
214 young (2.5-4.5 years old, $n = 18$) versus physically mature males (≥ 5.5 years old; $n = 41$).
215 We ranked models based on the Akaike Information Criterion with second-order adjustment (AICc)
216 to correct for small sample bias (Burnham and Anderson, 2002). The models with the lowest AICc
217 were considered to be the best models. We also computed Akaike weights (AICc weights) to
218 compare the relative performance of models rather than only their absolute AICc value (Burnham
219 and Anderson, 2002). Weights can be interpreted as the probability that a model is the best one
220 given the data and the set of candidate models. For comparisons of effect sizes, we considered non-
221 overlapping 95% confidence intervals as statistically different and provided p-values otherwise. We
222 performed all the statistical analyses using R 3.6.1 (R Core Team, 2020).

223

224

225 **3. Results**

226 The best supported model included the interaction between sex and period but no age effect within
227 males (Table 1). This model was 6 times more supported than the second best model (AICc weights
228 = 0.857 and 0.143, respectively) that included a difference in kidney fat between young and mature
229 males. All other models had no support (sum of their AICc weights close to 0; Table 1).

230 The best model supported sex-dependent kidney fat variation from the pre-rut to the post-rut period
231 (H1 and H3 supported), and a similar level and pattern of variation of kidney fat for both young and
232 mature males (Fig. 1; H2 not supported). According to this model, the average fat mass in females
233 was lowest during the pre-rut period (12.4g [8.3 – 18.4]_{95%}) and increased by 2–3 times during the
234 rut (23.7g [14.4 – 38.8]_{95%}) and the post-rut periods (36.5g [24.6 – 54.2]_{95%}; Fig. 1). Conversely, in
235 males, the average fat mass was maximum during the pre-rut period (42.9g [33.7 – 58.1]_{95%}) and
236 strongly decreased during the rut (10.7g [8.3 – 13.8]_{95%}) and the post-rut periods (15.1g [11.1 –
237 20.7]_{95%}). Compared with females, males had higher fat mass during the pre-rut period (3.5 times
238 higher), but lower values during the rut and post-rut periods (Fig. 1).

239 According to the second-best model, mature males would have a better condition than young ones
240 during the pre-rut period (53.5g [36.3; 79.0]_{95%} and 32.2g [20.6; 50.4]_{95%}, respectively; $p = 0.083$;
241 Appendix 1), while both categories would have a similar condition during the rut (10.8g [7.9;
242 14.8]_{95%} and 10.4g [6.7; 16.2]_{95%}, respectively; $p = 0.889$; during post-rut only two young males
243 were measured preventing us from statistical comparison). Therefore, this model would support a
244 higher decrease of fat mass between the pre-rut and rut periods in mature rather than in young
245 males, respectively.

246 **4. Discussion**

247 In agreement with our expectations (H1 and H3), the rutting period appeared to not be energetically
248 demanding for females compared with males, for which fat mass markedly drops during that period,
249 supporting the high energetic investment of males in rutting activities in this highly dimorphic
250 species. We also observed a similar pattern of fat mass changes in young and mature males, results

251 that also reveal a marked energetic investment of young males in rutting activities (in support of
252 H2) in this population facing selective harvesting of their old males (Garel et al., 2007).

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

275 During the rut, males experienced a marked decrease in their body condition (our results and e.g.,
276 Forsyth et al., 2005; Holand et al., 2006; Monteith et al., 2020; Rughetti and Festa-Bianchet, 2011).

277 These results support the hypothesis of a substantial cost of male reproduction in sexually
278 dimorphic capital breeders that mostly rely on body energetic reserves. These costs result from the
279 direct energy expenditure associated with rutting behaviors and from the reduced involvement in
280 feeding activities (Bon et al., 1995; Brivio et al., 2010; Clutton-Brock et al., 1982; Monteith et al.,
281 2020). Thus, costs may be higher than acquired energy and lead to a negative energetic balance and
282 to the metabolism of their fat reserves during this period. The tendency for mature males to have a
283 better condition compared with young ones before participating in rutting activities (second best
284 model; Appendix 1) may originate from a trade-off in the latter between accumulating body fat
285 while still being in a period of intensive body growth (Hamel et al., 2016).

286 While reproductive investment in ungulate males increases with age (Clutton-Brock, 1984; Clutton-
287 Brock et al., 1982; Garel et al., 2011; Mysterud et al., 2004), we observed comparable energetic
288 investments in both young and mature males. A high energetic investment of young males during
289 rut has been previously observed in populations of wild ungulates experiencing trophy hunting,
290 with large-horned or large antlered males being selectively targeted. In such populations, the biased
291 hunting pressure against mature, old males may lead to a female-biased adult sex ratio and a higher
292 proportion of young males compared with non-hunted populations. Where there is a lack of mature
293 males, young ones may then invest more energy in rutting activities and less so on body growth,
294 with potential short- and long-term consequences on their body mass, size, and survival (Bon et al.,
295 1992; Garel et al., 2006; Mysterud, 2014; Singer and Zeigenfuss, 2002). The studied population of
296 mouflon faced trophy hunting, which decreased the proportion of mature males (average age of
297 hunted males = 10.2 years, in 1996-2002; Garel et al., 2007), offering opportunities for young
298 individuals to be more involved in reproductive activities at similar levels to mature individuals
299 (Bon et al., 1995, 1992). Such hunting pressure might have contributed to the high energetic
300 investment of young males during the rut. However, further studies based on experimental design
301 (e.g. Monteith et al. 2020) or on larger sample sizes comparing populations of mouflon facing high
302 selective hunting pressures with non-hunted populations (acting as a control) would help to

303 definitively support this hypothesis. The observed marked energetic investment of young males
304 during the rut, while consistent with other knowledge on the influence of selective harvesting in this
305 population (on horns size and shape; Garel et al., 2007), questioned the long-term consequences
306 both in terms of survival and other fitness-related components (Festa-Bianchet et al., 2003; Forsyth
307 et al., 2005; Garel et al., 2009; Singer and Zeigenfuss, 2002; Stringham and Bubenik, 1975). This
308 result also supports the need for more empirical and comparative studies to better investigate the
309 potential side effects of selective hunting on the rutting ecology of male ungulates (Milner et al.,
310 2007).

311 **Acknowledgments**

312 The authors warmly thank all the hunters from FDC 34, GIEC, ONCFS – OFB and ONF for
313 collecting samples, the trainees for the analysis of samples and VetAgro Sup, LBBE and ONCFS
314 for their financial and logistic supports. The authors declare that they have no conflict of interest.

315 **References**

- 316 Anderson, A.E., 1981. Morphological and physiological characteristics., in: Mule and Black-Tailed Deer of
317 North America. univ. Nebraska Press, pp. 27–97.
- 318 Anderson, A.E., Bowden, D.C., Medin, E., 1990. Indexing the annual fat cycle in a mule deer population. J.
319 Wildl. Manag. 550–556.
- 320 Andersson, M.B., 1994. Sexual selection. Princeton University Press, Princeton, N.J.
- 321 Baudière, A., 1962. Le Parc National du Caroux – essai de synthèse climatique. 33, 169–186.
- 322 Bon, R., Dardaillon, M., Estevez, I., 1993. Mating and lambing periods as related to age of female mouflon.
323 J. Mammal. 74, 752–757.
- 324 Bon, R., Gonzalez, G., Bosch, M.D., Cugnasse, J.-M., 1992. Ram rut-involvement in a hunted population of
325 mouflons. Acta Theriol. (Warsz.) 37, 63–71.
- 326 Bon, R., Recarte, J.M., Gonzalez, G., Cugnasse, J.-M., 1995. Courtship and behavioral maturation of male
327 mouflons. Acta Theriol. (Warsz.) 40, 283–294.
- 328 Bourgoin, G., Garel, M., Blanchard, P., Dubray, D., Maillard, D., Gaillard, J.-M., 2011. Daily responses of
329 mouflon (*Ovis gmelini musimon* × *Ovis* sp.) activity to summer climatic conditions. Can. J. Zool. 89,
330 765–773.
- 331 Bourgoin, G., Marchand, P., Hewison, A.M., Ruckstuhl, K.E., Garel, M., 2018. Social behaviour as a
332 predominant driver of sexual, age-dependent and reproductive segregation in Mediterranean
333 mouflon. Anim. Behav. 136, 87–100.
- 334 Brivio, F., Grignolio, S., Apollonio, M., 2010. To feed or not to feed? Testing different hypotheses on rut-
335 induced hypophagia in a mountain ungulate. Ethology 116, 406–415.
- 336 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-
337 theoretic approach. Springer Science & Business Media.
- 338 Byers, J.A., Waits, L., 2006. Good genes sexual selection in nature. Proc. Natl. Acad. Sci. 103, 16343–16345.
- 339 Carranza, J., Alvarez, F., Redondo, T., 1990. Territoriality as a mating strategy in red deer. Anim. Behav. 40,
340 79–88. [https://doi.org/10.1016/S0003-3472\(05\)80667-0](https://doi.org/10.1016/S0003-3472(05)80667-0)
- 341 Caughley, G., 1970. Fat reserves of Himalayan thar in New Zealand by season, sex, area and age. N. Z. J. Sci.
342 13, 209–219.
- 343 Clutton-Brock, T.H., 1989. Mammalian mating systems. Proc. R. Soc. Lond. B Biol. Sci. 236, 339–372.
- 344 Clutton-Brock, T.H., 1984. Reproductive effort and terminal investment in iteroparous animals. Am. Nat.
345 123, 212–229. <https://doi.org/10.1086/284198>
- 346 Clutton-Brock, T.H., Albon, S.D., Guinness, F.E., 1989. Fitness costs of gestation and lactation in wild
347 mammals. Nature 337, 260–262.
- 348 Clutton-Brock, T.H., Albon, S.D., Guinness, F.E., 1988. Reproductive success in male and female red deer, in:
349 Reproductive Success. Univ. Chicago Press, Chicago, Ill. Clutton-Brock, T. H., University of Chicago,
350 Chicago, Illinois, USA, pp. 325–343.
- 351 Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982. Red deer: behavior and ecology of two sexes.
352 University of Chicago press.
- 353 Clutton-Brock, T.H., Price, O.F., MacColl, A.C., 1992. Mate retention, harassment, and the evolution of
354 ungulate leks. Behav. Ecol. 3, 234–242.
- 355 Cransac, N., Hewison, A.J.M., Maublanc, M.-L., Gaillard, J.-M., Cugnasse, J.-M., 1997. Patterns of mouflon
356 (*Ovis gmelini*) survival under moderate environmental conditions: effects of sex, age, and
357 epizootics. Can. J. Zool. 75, 1867–1875.
- 358 Doughty, P., Shine, R., 1997. Detecting life history trade-offs: measuring energy stores in “capital” breeders
359 reveals costs of reproduction. Oecologia 110, 508–513. <https://doi.org/10.1007/s004420050187>
- 360 Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197,
361 215–223.
- 362 Festa-Bianchet, M., Gaillard, J.-M., Côté, S.D., 2003. Variable age structure and apparent density
363 dependence in survival of adult ungulates. J. Anim. Ecol. 72, 640–649.
- 364 Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., 1998. Mass-and density-dependent reproductive success
365 and reproductive costs in a capital breeder. Am. Nat. 152, 367–379.

366 Foley, A.M., Hewitt, D.G., DeYoung, R.W., Schnupp, M.J., Hellickson, M.W., Lockwood, M.A., 2018.
367 Reproductive effort and success of males in scramble-competition polygyny: Evidence for trade-offs
368 between foraging and mate search. *J. Anim. Ecol.* 87, 1600–1614.

369 Forsyth, D.M., Duncan, R.P., Tustin, K.G., Gaillard, J.-M., 2005. A substantial energetic cost to male
370 reproduction in a sexually dimorphic ungulate. *Ecology* 86, 2154–2163.

371 Garel, M., Cugnasse, J.-M., Gaillard, J.-M., Loison, A., Gibert, P., Douvre, P., Dubray, D., 2005a. Reproductive
372 output of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.): a comparative analysis. *J. Zool.* 266,
373 65–71.

374 Garel, M., Cugnasse, J.-M., Maillard, D., 2005b. Reliability of mouflon aging using morphological
375 characteristics from observations in the field. *Wildl. Biol.* 11, 229–235.

376 Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A.J., Dubray, D., 2007. Selective harvesting
377 and habitat loss produce long-term life history changes in a mouflon population. *Ecol. Appl.* 17,
378 1607–1618.

379 Garel, M., Forsyth, D.M., Loison, A., Dubray, D., Jullien, J.-M., Tustin, K.G., Maillard, D., Gaillard, J.-M., 2011.
380 Age-related male reproductive effort in two mountain ungulates of contrasting sexual size
381 dimorphism. *Can. J. Zool.* 89, 929–937.

382 Garel, M., Loison, A., Gaillard, J.-M., Cugnasse, J.-M., Maillard, D., 2004. The effects of a severe drought on
383 mouflon lamb survival. *Proc. R. Soc. Lond. B Biol. Sci.* 271, S471–S473.

384 Garel, M., Solberg, E.J., Sæther, B., Grøtan, V., Tufto, J., Heim, M., 2009. Age, size, and spatiotemporal
385 variation in ovulation patterns of a seasonal breeder, the norwegian moose (*Alces alces*). *Am. Nat.*
386 173, 89–104. <https://doi.org/10.1086/593359>

387 Garel, M., Solberg, E.J., Sæther, B.-E., Herfindal, I., Høgda, K.-A., 2006. The length of growing season and
388 adult sex ratio affect sexual size dimorphism in moose. *Ecology* 87, 745–758.

389 Geist, V., 1966. Validity of horn segment counts in aging bighorn sheep. *J. Wildl. Manag.* 634–635.

390 Gittleman, J.L., Thompson, S.D., 1988. Energy allocation in mammalian reproduction. *Am. Zool.* 28, 863–
391 875.

392 Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Albon, S., Côté, S.D., Craine, J.M., Festa-Bianchet, M., Garel, M., Lee,
393 P., Moss, C., Nussey, D.H., Pelletier, F., Stien, A., Tveraa, T., 2016. Cohort variation in individual
394 body mass dissipates with age in large herbivores. *Ecol. Monogr.* 86, 517–543.
395 <https://doi.org/10.1002/ecm.1232>

396 Hewison, A.J.M., Gaillard, J.M., 2001. Phenotypic quality and senescence affect different components of
397 reproductive output in roe deer. *J. Anim. Ecol.* 70, 600–608. <https://doi.org/10.1046/j.1365-2656.2001.00528.x>

399 Hogg, J.T., Forbes, S.H., 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk
400 “unconventional” tactic. *Behav. Ecol. Sociobiol.* 41, 33–48. <https://doi.org/10.1007/s002650050361>

401 Holand, Ø., Weladji, R.B., Røed, K.H., Gjøstein, H., Kumpula, J., Gaillard, J.-M., Smith, M.E., Nieminen, M.,
402 2006. Male age structure influences females’ mass change during rut in a polygynous ungulate: the
403 reindeer (*Rangifer tarandus*). *Behav. Ecol. Sociobiol.* 59, 682–688.

404 Isvaran, K., 2005. Variation in male mating behaviour within ungulate populations: patterns and processes.
405 *Curr. Sci.* 89, 1192–1199.

406 Jönsson, K.I., 1997. Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction.
407 *Oikos* 78, 57–66. <https://doi.org/10.2307/3545800>

408 Knopp, R.H., Saudek, C.D., Arky, R.A., O’Sullivan, J.B., 1973. Two phases of adipose tissue metabolism in
409 pregnancy: maternal adaptations for fetal growth. *Endocrinology* 92, 984–988.

410 Lincoln, G.A., 1998. Reproductive seasonality and maturation throughout the complete life-cycle in the
411 mouflon ram (*Ovis musimon*). *Anim. Reprod. Sci.* 53, 87–105. [https://doi.org/10.1016/S0378-4320\(98\)00129-8](https://doi.org/10.1016/S0378-4320(98)00129-8)

412

413 Loudon, A.S.I., 1985. Lactation and neonatal survival of mammals, in: *Symposia of the Zoological Society of*
414 *London.* pp. 183–207.

415 Mainguy, J., Côté, S.D., Cardinal, E., Houle, M., 2008. Mating tactics and mate choice in relation to age and
416 social rank in male mountain goats. *J. Mammal.* 89, 626–635. <https://doi.org/10.1644/07-MAMM-A-234R.1>

417

- 418 Marchand, P., Garel, M., Bourgoïn, G., Dubray, D., Maillard, D., Loison, A., 2015. Coupling scale-specific
419 habitat selection and activity reveals sex-specific food/cover trade-offs in a large herbivore. *Anim.*
420 *Behav.* 102, 169–187.
- 421 Marchand, P., Garel, M., Bourgoïn, G., Dubray, D., Maillard, D., Loison, A., 2014. Sex-specific adjustments in
422 habitat selection contribute to buffer mouflon against summer conditions. *Behav. Ecol. aru212.*
- 423 McElligott, A.G., Naulty, F., Clarke, W.V., Hayden, T.J., 2003. The somatic cost of reproduction: what
424 determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.*
- 425 Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in
426 ungulates and carnivores. *Conserv. Biol.* 21, 36–47.
- 427 Miquelle, D.G., 1990. Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27, 145–151.
- 428 Monteith, K.L., Monteith, K.B., Jenks, J.A., Jakopak, R.P., 2020. One in the hand worth two in the bush?
429 Reproductive effort of young males is not affected by the presence of adult males. *Front. Ecol. Evol.*
430 8. <https://doi.org/10.3389/fevo.2020.00274>
- 431 Moore, N.P., Kelly, P.F., Cahill, J.P., Hayden, T.J., 1995. Mating strategies and mating success of fallow
432 (*Dama dama*) bucks in a non-lekking population. *Behav. Ecol. Sociobiol.* 36, 91–100.
433 <https://doi.org/10.1007/BF00170713>
- 434 Mysterud, A., 2014. Effects of selective harvesting on ungulate populations, in: *Behaviour and Management*
435 *of European Ungulates.*
- 436 Mysterud, A., Bonenfant, C., Loe, L.E., Langvatn, R., Yoccoz, N.G., Stenseth, N.C., 2008. Age-specific feeding
437 cessation in male red deer during rut. *J. Zool.* 275, 407–412.
- 438 Mysterud, A., Holand, Ø., Røed, K.H., Gjøstein, H., Kumpula, J., Nieminen, M., 2003. Effects of age, density
439 and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *J. Zool.* 261, 341–344.
- 440 Mysterud, A., Langvatn, R., Stenseth, N.C., 2004. Patterns of reproductive effort in male ungulates. *J. Zool.*
441 264, 209–215.
- 442 Mysterud, A., Solberg, E.J., Yoccoz, N.G., 2005. Ageing and reproductive effort in male moose under
443 variable levels of intrasexual competition. *J. Anim. Ecol.* 74, 742–754.
444 <https://doi.org/10.1111/j.1365-2656.2005.00965.x>
- 445 Oftedal, O.T., 1985. Pregnancy and lactation, in: *Bioenergetics of Wild Herbivores.* CRC Press, Boca Raton,
446 FL, pp. 215–238.
- 447 Pelletier, F., Hogg, J.T., Festa-Bianchet, M., 2006. Male mating effort in a polygynous ungulate. *Behav. Ecol.*
448 *Sociobiol.* 60, 645–654. <https://doi.org/10.1007/s00265-006-0208-y>
- 449 Pelletier, F., Mainguy, J., Côté, S.D., 2009. Rut-induced hypophagia in male Bighorn sheep and Mountain
450 goats: foraging under time budget constraints. *Ethology* 115, 141–151.
- 451 Pérez-Barbería, F.J., Mutuberria, G., Nores, C., 1998. Reproductive parameters, kidney fat index, and
452 grazing activity relationships between the sexes in Cantabrian chamois *Rupicapra pyrenaica parva*.
453 *Acta Theriol. (Warsz.)* 43, 311–324.
- 454 R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical
455 Computing, Vienna, Austria.
- 456 Ralls, K., 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* 917–
457 938.
- 458 Rieck, W., 1975. Muffelwildalter (Brochure de l'association des chasseurs d'Allemagne Fédérale). Bonn,
459 Germany (In German).
- 460 Riney, T., 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to
461 New Zealand. *J. Sci. Technol.* 36, 429–463.
- 462 Robert, T., 1972. Parental investment and sexual selection. *Sex. Sel. Descent Man Aldine Gruyter N. Y.* 136–
463 179.
- 464 Rughetti, M., Festa-Bianchet, M., 2011. Seasonal changes in sexual size dimorphism in northern chamois. *J.*
465 *Zool.* 284, 257–264.
- 466 Santiago-Moreno, J., Brunet, A.G., Bulnes, A.G. de, Villar, D., Sebastian, A.L., 2000. Attainment of puberty in
467 the European mouflon (*Ovis gmelini musimon*) and the domestic Manchega ewe (*Ovis aries*).
468 *Reprod. Domest. Anim.* 35, 49–52. <https://doi.org/10.1046/j.1439-0531.2000.00195.x>
- 469 Serrano, E., Alpizar-Jara, R., Morellet, N., Hewison, A.J.M., 2008. A half a century of measuring ungulate
470 body condition using indices: is it time for a change? *Eur. J. Wildl. Res.* 54, 675–680.

471 Singer, F.J., Zeigenfuss, L.C., 2002. Influence of trophy hunting and horn size on mating behavior and
472 survivorship of mountain sheep. *J. Mammal.* 83, 682–698.

473 Stearns, S.C., 1992. *The evolution of life histories*. Oxford University Press, Oxford.

474 Stringham, S., Bubenik, A., 1975. Physical condition and survival rate of chamois (*Rupicapra rupicapra* L) as
475 a function of maturity-sex class ratios in the population: implications for ungulate harvest plans.
476 *Bull. Off. Chasse Etudes Sci. Tech.* 3, 199–224.

477 Weckerly, F.W., 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic
478 mammals. *J. Mammal.* 79, 33–52. <https://doi.org/10.2307/1382840>

479 Weladji, R.B., Mysterud, A., Holand, Ø., Lenvik, D., 2002. Age-related reproductive effort in reindeer
480 (*Rangifer tarandus*): evidence of senescence. *Oecologia* 131, 79–82.
481 <https://doi.org/10.1007/s00442-001-0864-6>

482 Willisich, C.S., Neuhaus, P., 2009. Alternative mating tactics and their impact on survival in adult male alpine
483 ibex (*Capra ibex ibex*). *J. Mammal.* 90, 1421–1430. <https://doi.org/10.1644/08-MAMM-A-316R1.1>

484 Yoccoz, N.G., Mysterud, A., Langvatn, R., Stenseth, N.C., 2002. Age- and density-dependent reproductive
485 effort in male red deer. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 1523–1528.

486

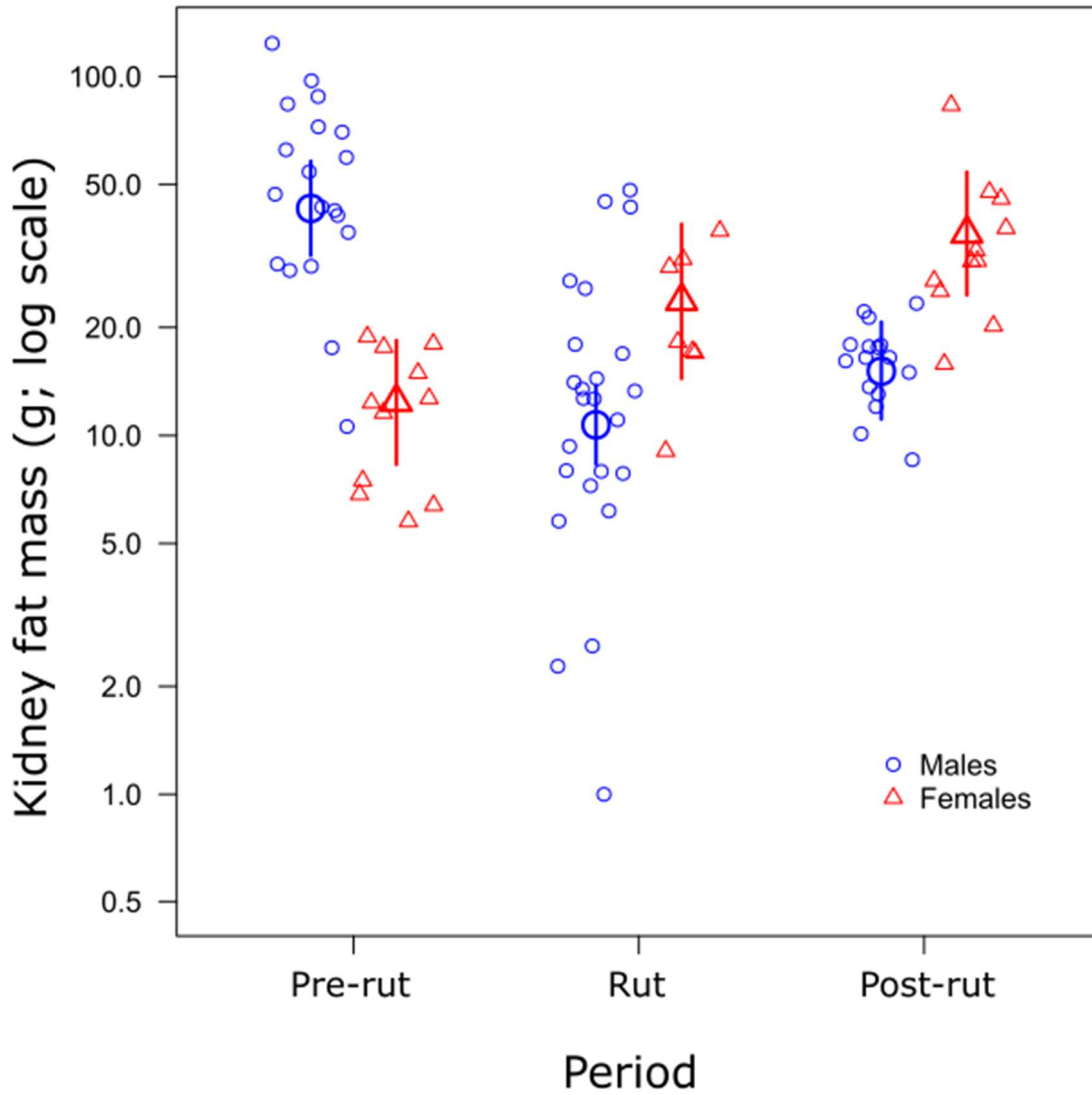
487 **Table 1:** Selection of linear models based on corrected Akaike's Information Criterion (AICc) for
 488 testing the effects of the sex (females, males) or age_sex (females, young males, mature males)
 489 factors and of the period (pre-rut, rut, post-rut) on the fat mass of kidneys (log-transformed) from
 490 mouflon harvested in the Caroux-Espinouse massif, France, period 2011-2012. All models included
 491 the log-transformed kidney mass as a covariate (Serrano et al., 2008).

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

492

493 **Figures**

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



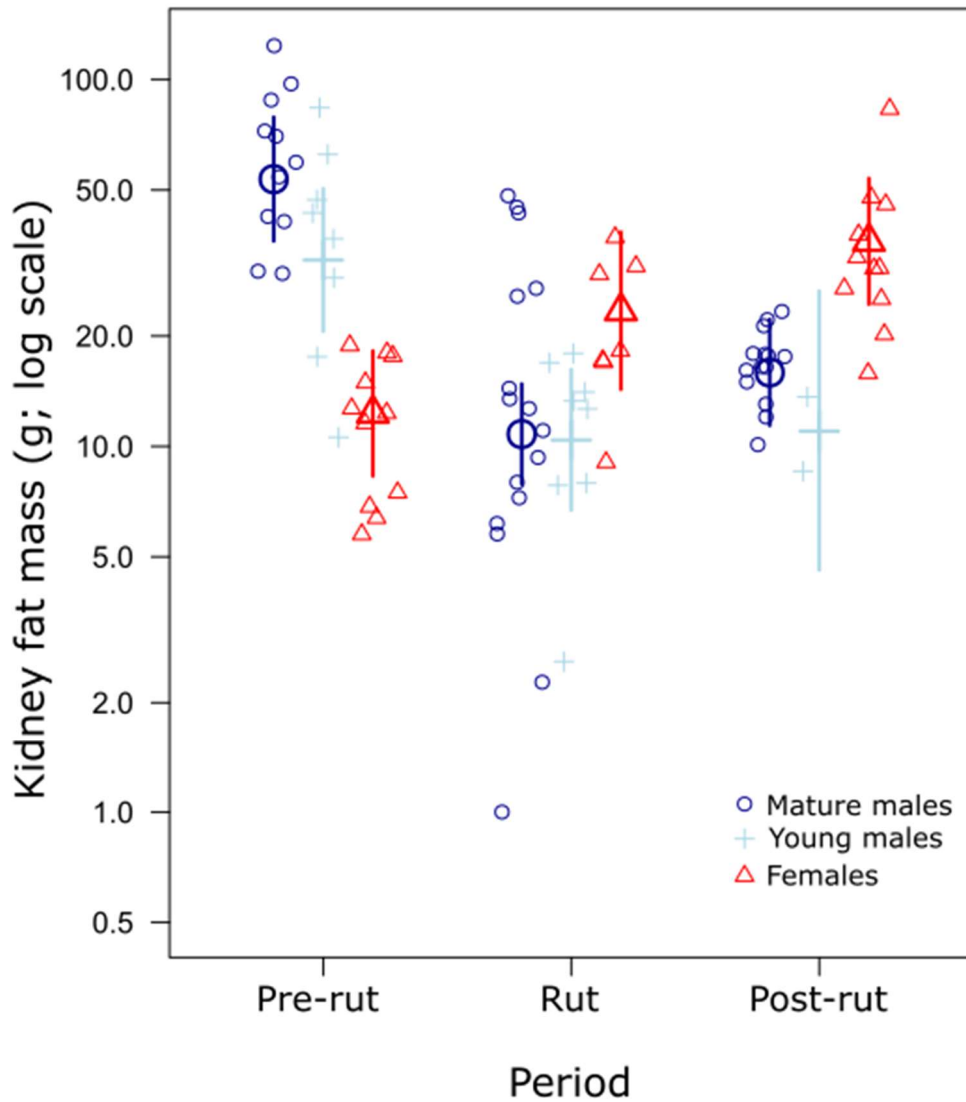
497

498

Appendix 1

500 **Figure 1:** Predicted values with 95% confidence intervals of mean kidney fat mass, and observed
501 data, for mature and young male and female mouflon from the Caroux-Espinouse massif (southern
502 France), for each period of 2 months during the September 2011 – February 2012 period, based on
503 the second best model.

504



505

506