Age-related male reproductive effort in two mountain ungulates of contrasting sexual size dimorphism

M. Garel, D.M. Forsyth, A. Loison, D. Dubray, J.-M. Jullien, K.G. Tustin, D. Maillard, and J.-M. Gaillard

Abstract: In polygynous ungulates, the reproductive effort of adult males peaks during a short period in which feeding activities are sacrificed for mating activities. Hence, both fat reserves and body mass are predicted to decline markedly during this period. The decline is also predicted to be greater in fat reserves than in body mass because fat is catabolized before muscle, and to increase with the intensity of sexual selection. In contrast, no specific patterns are expected in females for which late gestation and lactation rather than mating are the energetically most demanding periods. We tested these hypotheses in two mountain ungulates of contrasting sexual size dimorphism (SSD): Himalayan tahr (*Hemitragus jemlahicus* (H. Smith, 1826)) (SSD = 123%) and alpine chamois (*Rupicapra rupicapra* (L., 1758)) (SSD = 26%). As expected, kidney fat declined more rapidly than body mass in adult males of both species. Kidney fat declined faster in adult male tahr compared with adult male chamois. There was no consistent pattern of changes in body mass or kidney fat in female tahr or female chamois. Our results suggest that adult males of species with strong SSD allocate more energy to mating than males of less dimorphic species.

Résumé : Chez les ongulés polygynes, l'effort de reproduction des mâles adultes atteint son maximum durant une courte période pendant laquelle les activités alimentaires sont sacrifiées en faveur des activités de reproduction. Les réserves de graisses et la masse corporelle devraient donc diminuer fortement durant cette période. Ce déclin devrait être plus marqué pour les réserves de graisses que pour la masse corporelle car la graisse est catabolisée avant le muscle. Ce déclin devrait aussi augmenter avec l'intensité de la sélection sexuelle. En revanche, aucun patron spécifique n'est attendu chez les femelles pour qui la fin de la gestation et l'allaitement sont les périodes les plus coûteuses en énergie. Nous avons testé ces hypothèses chez deux ongulés de montagne présentant un dimorphisme sexuel de taille (SSD) très contrasté : le thar de l'Himalaya (*Hemitragus jemlahicus* (H. Smith, 1826)) (SSD = 123 %) et le chamois (*Rupicapra rupicapra* (L., 1758)) (SSD = 26 %). Comme attendu, les graisses rénales ont diminué plus rapidement que la masse corporelle chez les mâles adultes des deux espèces et ces graisses ont diminué plus rapidement chez les mâles adultes de thar que chez les males adultes de chamois. Nous n'avons pas détecté de patron de variation spécifique de la masse corporelle et des graisses rénales chez les femelles de thar et de chamois. Nos résultats indiquent que les mâles adultes des espèces à fort SSD allouent plus d'énergie à la reproduction que les mâles d'espèces moins dimorphiques en taille.

Introduction

Sexual size dimorphism (SSD) is mostly thought to have evolved from sexual selection through intra-sex competition or mate choice (Andersson 1994). Emlen and Oring (1977) proposed that males should be sexually selected for gaining increased access to females and females should compete for access to food. Consequently, males undergo rapid growth for many years to attain the large size that enables them to obtain matings, whereas females favour high body condition and early sexual maturity at the expense of structural size

(Andersson 1994). In polygynous ungulates, larger males should obtain greater reproductive success than smaller males by being able to allocate relatively more energy in intra-sexual competition such as fights, mate-guarding, territorial behaviour (e.g., defence of good food patches where females stand), or tending (Clutton-Brock 1989; Clutton-Brock et al. 1992; Pelletier et al. 2006), and by being more attractive to females (Byers and Waits 2006). In addition, most of the reproductive effort of polygynous males occurs during a relatively short rut, during which feeding activities are usually sacrificed for mating activities (Clutton-Brock et al.

M. Garel, D. Dubray, J.-M. Jullien, and D. Maillard. Office National de la Chasse et de la Faune Sauvage, Centre National d'Étude et de Recherche Appliquée sur la Faune de Montagne, Portes du soleil, 147 route de Lodève, F-34990 Juvignac, France.
D.M. Forsyth. Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, 123 Brown Street, Heidelberg, Victoria 3084, Australia.
A. Loison. Laboratoire d'Écologie Alpine (LECA), CNRS, UMR 5553, Université de Savoie, F-73376 Le Bourget du Lac, France.
K.G. Tustin. Bull Creek Road, RD, Milton 9292, Otago, New Zealand.
J.-M. Gaillard. Université de Lyon, F-69000 Lyon; Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France.

Corresponding author: M. Garel (e-mail: mathieu.garel@oncfs.gouv.fr).

1982). In contrast, late gestation and lactation (during the spring–summer for temperate species) rather than mating (in summer–autumn for temperate species) are the energetically most demanding periods for females (Clutton-Brock et al. 1989). In addition, females do not stop feeding during the rut and should therefore experience less mass change than males (Clutton-Brock et al. 1982). These changes will principally depend on environmental conditions encountered, and to some extent to the level of harassment by males, leading to the different patterns (i.e., increasing, decreasing, or steady body mass) that have been reported in the literature (e.g., Mysterud et al. 2001; Forsyth et al. 2005; Holand et al. 2006).

Although many studies have investigated patterns of variation in reproductive effort for female ungulates (e.g., red deer (*Cervus elaphus* L., 1758): Clutton-Brock et al. 1989; bighorn sheep (*Ovis canadensis* Shaw, 1804): Festa-Bianchet et al. 1998; moose (*Alces alces* (L., 1758)): Sand 1998; roe deer (*Capreolus capreolus* (L., 1758)): Hewison and Gaillard 2001; reindeer (*Rangifer tarandus* L., 1758): Weladji et al. 2002), fewer studies have quantified male reproductive effort (reviewed in Mysterud et al. 2004). Female reproductive effort can be evaluated through the production of young, but male reproductive effort results from multiple components that are difficult to measure (e.g. fighting, patrolling territories, vocalizations, and tending females; Mysterud et al. 2004). Published studies (red deer: Yoccoz et al. 2002; moose: Mysterud et al. 2005) have often used changes in body mass to estimate the energetic costs of male reproductive effort. As predicted, male energetic loss during rut in these species was age-dependent, as was the involvement of males in rutting activities. However, the extent of male energetic expenditure is also expected to be related to the extent of male–male competition, and should therefore vary among and even within species (Lott 1991).

As the strength of selection for SSD seems mostly related to the intensity of competition among males in ungulates (Loison et al. 1999b), reproduction should involve the largest energetic costs for males in species with the largest SSD. Here, we test hypotheses about intra- and inter-specific male reproductive effort in two contrasting mountain ungulates: the alpine chamois (*Rupicapra rupicapra* (L., 1758)) in which adult males are about 25% larger than adult females and the Himalayan tahr (*Hemitragus jemlahicus* (H. Smith, 1826)) in which adult males are about 125% larger than adult females (see Results below for species-specific estimates of SSD). Although previous studies have relied on measures of body mass only, less is known about how fat changes over the mating period (but see Forsyth et al. 2005). Fat could be a more sensitive measure of energetic costs of reproduction because it is catabolized prior to body mass owing to its high energy content (Pond 1998). We thus combined data on changes over time of both body mass and kidney fat to assess the relative sensitivity of these measures of energetic costs. In ungulates, kidney fat reserves are known to be a reliable measure of total body fat over a large range of food conditions (Riney 1955; Caughley 1970), and can thus be used as a measure of stored energy to investigate variation in reproductive effort among age classes, sexes, and species. The energetic demands of female tahr and female chamois during the mating period are not expected to change with increasing age. In contrast, the reproductive costs of male tahr and male chamois within the mating period should increase with age, as previously reported for tahr (study on fat only: Forsyth et al. 2005) and for males of other ungulates species (e.g., red deer: Yoccoz et al. 2002; moose: Mysterud et al. 2005; reviewed in Mysterud et al. 2004). We predicted that adult male tahr would undergo a greater decline in both body mass and fat reserves than adult male chamois because of the much larger SSD in tahr, but that the pattern would be similar in females of both species because female reproductive effort should remain similar irrespective of SSD. Finally, we predicted that fat reserves would decline faster than body mass in adult male of both tahr and chamois.

Materials and methods

Study areas and species

Alpine chamois were studied in the Bauges National Reserve (45°40′N, 6°13′E; 700–2217 m above sea level; 5205 ha), northern French Alps. The Bauges mountains are a subalpine massif of 86 000 ha covered by forests up to about 1500 m and by cliffs and open grasslands between 1700 and 2200 m. Himalayan tahr were sampled from 18 areas in the Southern Alps, South Island, New Zealand (43°34′S, 170°10′E; 750–2250 m above sea level; 425 900 ha; Forsyth and Tustin 2005). Animals generally inhabit rock bluff systems, the adjacent snow tussock basins, and alpine grasslands (Forsyth 2000). For further information on study areas and populations see Loison et al. (1999c) for chamois and Forsyth and Tustin (2005) for tahr.

Data

Data were collected from animals harvested in 1997–2002 and 1972–1976 for chamois and tahr, respectively (see Appendix A, Figs. A1–A4). In the Bauges National Reserve, chamois were hunted from early September to the end of February and hunting was controlled by hunting guides; in the Southern Alps, tahr were shot by commercial helicopter-based hunters from early May to the end of September. In the two species, 22 cohorts were sampled.

Age determination of both sexes was based on counts of horn growth annuli (tahr: Caughley 1965; chamois: Schröder and Von Elsner-Schak 1985). In both species, we used the mass ($\pm$1 g) of fat stored around the kidneys as an indicator of body condition (Riney 1955). In chamois, fat mass was not consistently taken for the two kidneys (9% of animals with only one kidney). However, based on animals for which the two kidneys were measured, there was no difference in the fat mass and the mass of the left and right kidneys (paired t tests, $t_{[296]} = -0.38$, $P = 0.70$ and $t_{[296]} = 0.70$, $P = 0.48$, respectively). We thus included animals with only data on one kidney in our analyses. For tahr, carcass mass ($\pm$100 g) was calculated as the eviscerated, hocked, and beheaded carcass mass minus all bleedable blood. For chamois, the measurements of carcass mass ($\pm$100 g) were made in three ways: (1) full carcass mass (including rumen content), (2) eviscerated carcass mass minus bleedable blood, or (3) partially eviscerated carcass mass with heart, liver, and lungs present. Based on chamois for which at least two different measures of mass were taken, we examined relationships between eviscerated carcass mass (most frequently measured) and the two other masses (see Garel et al. 2009a).

Because there were strong positive relationships ($r^2 > 0.95$), we transformed all other measures into eviscerated carcass mass.

Analyses

To estimate the difference in SSD between species, we performed an ANOVA on log-transformed carcass mass of >4.5-year-old chamois ($n = 149$ females and $n = 45$ males) and tahr ($n = 510$ females and $n = 185$ males). We used animals >4.5 years old for this analysis because this was when most (>90%) of the total body mass in both sexes was reached (Forsyth et al. 2005; Garel et al. 2009a) and when sample sizes were still large enough to obtain reliable estimates. Before estimating SSD, carcass masses were first adjusted to the start of rut in both species using linear models (see Julian dates below and Appendix A, Figs. A1 and A2).

We distinguished three age classes in both chamois and tahr of both sexes based on reproductive behaviour. In the following, age classes are defined as the exact age in years. Male tahr produce sperm and father offspring by 2.5 years, but full breeding pelage is not attained until 4.5 years (Forsyth and Tustin 2005). Although males younger than 2.5 years have not been observed engaging in reproductive behaviour (Forsyth et al. 2005) and cannot be included as adults ("reproductively immature"), "young adults" aged 2.5–4.5 years engage in the alternative mating tactic of coursing and "prime-aged" males >4.5 years engage primarily in tending and blocking behaviour to maintain exclusive access to oestrous females (sensu Clutton-Brock 1989). Chamois also use a tending mating system (Loison 1995) and we used the same age classes as for tahr (i.e., 0.5–1.5 years, 2.5–4.5 years, and >4.5 years). Based on the pregnancy rates of tahr (Forsyth et al. 2004) and chamois (Houssin et al. 1993), we defined the following age classes for females: none pregnant ("juveniles", 0.5 year); about half of the females pregnant ("yearlings", 1.5 years; 50.9% in thar and 63.3% in chamois); and most females pregnant ("adults", >1.5 years; 92.5% in chamois and 94.1% in tahr).

Harvest date was transformed to Julian date with 5 May and 5 September being day 1 in tahr and chamois, respectively. We accounted for the difference of 1 day in the leap year (e.g., 5 May is day 2 in a leap year). Given a median birth date of 30 November (Caughley 1971) and gestation length of 180 days (Hayssen et al. 1993), the peak of the tahr mating season should be around 4 June (day 31). Field observations of both mating behaviour and timing of births suggest 15 December (day 102) to be the peak of the chamois mating season in the Bauges National Reserve (Loison 1995). Based on these estimates and subsequent data analyses (Appendix A, Figs. A1–A4), we estimated the mating period in both species to encompass 61 days centred on the peak of rut (from 5 May to 4 July in tahr and from 15 November to 14 January in chamois).

We used carcass and fat masses as response variables. When modelling fat mass, we included kidney mass as a covariate (Serrano et al. 2008). Carcass, kidney, and fat masses were log-transformed ($y + 1$ for fat mass owing to the presence of zero values) to account for allometric relationships between kidney and fat masses, to normalize distributions, and to obtain residuals with constant variance. Transforming

Table 1. Parameter estimates from a linear model ($r^2 = 0.87$) including the log-transformed carcass mass of >4.5-year-old animals as a response variable and sex and species (alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*)) as predictors.

Parameter	b	SE	p
Intercept	3.069	0.012	<0.001
Sex (male)	0.229	0.024	<0.001
Species (tahr)	0.185	0.014	<0.001
Sex (male) × species (tahr)	0.573	0.027	<0.001

response variables also enable rates of changes to be compared on the same scale for different species and variables.

We first fitted a model to account for variation in carcass and fat masses over the whole sampling period and estimated the predicted values of carcass and fat masses at the start ($\hat{y}_{start}$) and at the end ($\hat{y}_{end}$) of the mating season. To capture the nonlinear relationship between carcass and fat masses and sampling date, we fitted models including sampling date along with its polynomial terms up to the fourth order (Appendix A, Figs. A1–A4; Forsyth et al. 2005). Model selection was based on Akaike's information criterion (AIC) with second-order adjustment (AIC_c) to correct for small sample bias (Burnham and Anderson 2002). The most parsimonious model (i.e., lowest AIC_c) was selected as the best model. Second, we assumed a linear relationship between response variables and sampling date to account for changes within the mating period (Bobek et al. 1990). Using the predicted values, we estimated slope as $(\hat{y}_{end} - \hat{y}_{start})/(x_{end} - x_{start})$, with x_{start} and x_{end} corresponding to sampling date at the start and at the end of the mating period, respectively. Third, to assess the uncertainty around the estimated slope, we simulated new data based on resampling of the original data for each age and sex class. We again fitted the polynomial models originally selected to obtain a new estimate of the slope; this procedure was replicated 1000 times. From the bootstrap distribution, we computed mean slopes and 95% confidence intervals (CIs) (i.e., 2.5% and 97.5% quantiles). Tests of our hypotheses were performed by comparing parameter distributions. Because we formulated specific predictions when comparing estimates (see Introduction above), we reported one-sided p values. Slopes were considered different when their 95% CIs did not overlap. Conversely, slopes were not retained as statistically significant when their 95% CIs included 0. Although we could have used mixed models with cohort and year of harvest as random factors, we chose to use models without random effects. Indeed, we had few fat mass data ($n < 25$) for some sex and age classes in chamois (see Appendix A, Fig. A3), making the estimation of additional parameters (i.e., random variances) questionable. Moreover, for all other combinations of data in which we had larger sample sizes, we obtained the same qualitative results with or without mixed models (results not presented here). All analyses were performed using R version 2.11.1 (R Development Core Team 2007).

Results

Sexual size dimorphism

Adult male chamois weighed 25.8% more than adult fe-

Fig. 1. Estimated changes (slopes with 95% confidence intervals (CIs)) in the kidney fat (●) and carcass masses (○; measurements were log-transformed) during the mating period in Himalayan tahr (*Hemitragus jemlahicus*) and alpine chamois (*Rupicapra rupicapra*), according to sex and age classes. The slope is equal to zero when there was no fat mass or carcass mass change during the mating period (see Appendix A, Figs. A1–A4). The top three panels describe males (M): immatures (1; 0.5 and 1.5 years), young adults (2; 2.5, 3.5, and 4.5 years), and prime-aged adults (3; >4.5 years). The bottom three panels describe females (F): immatures (1; 0.5 year), young adults (2; 1.5 years), and prime-aged adults (3; >1.5 years).
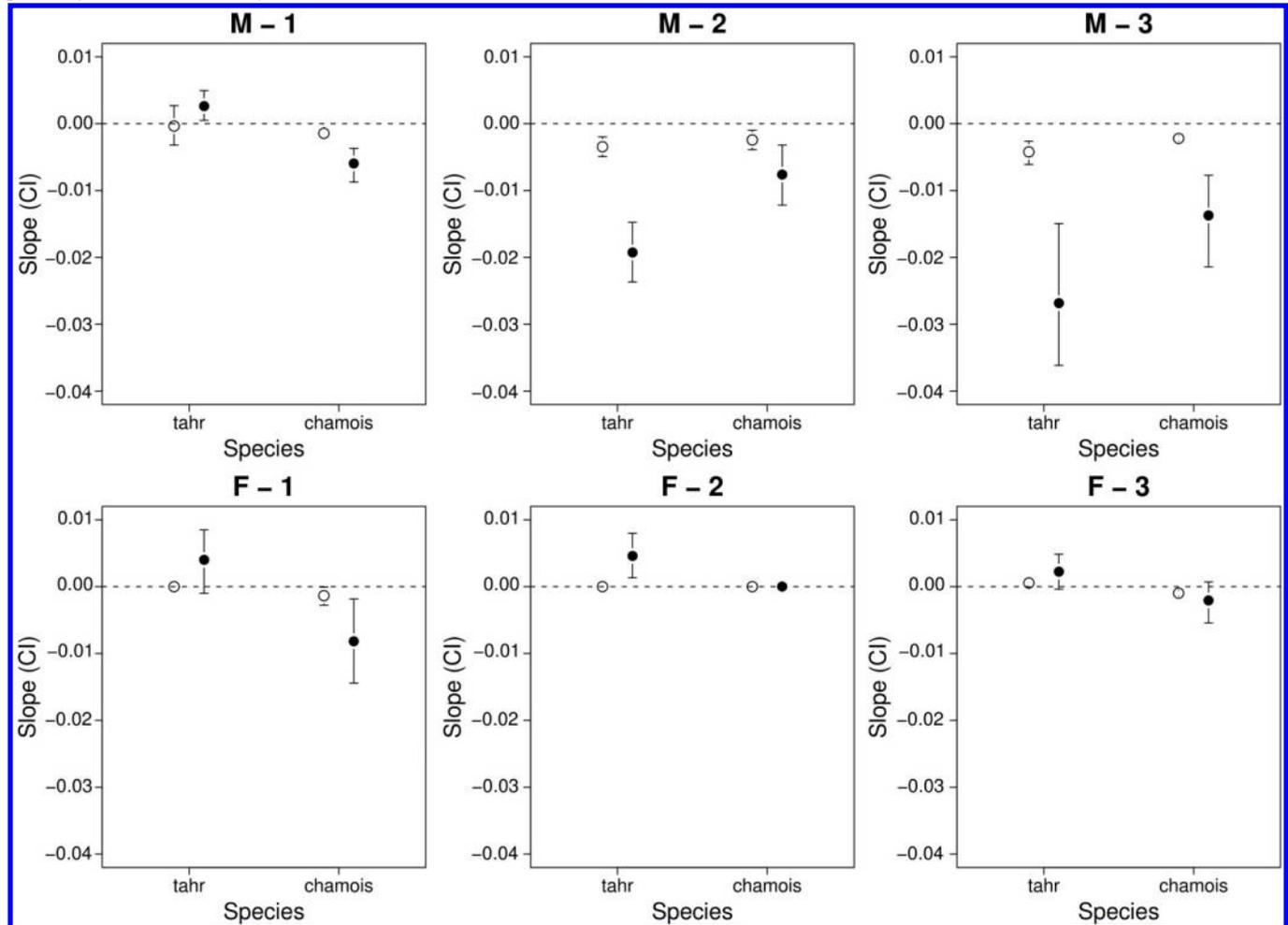
male chamois (observed mean ± SD; 27.2 ± 2.7 vs. 21.7 ± 2.6 kg), whereas adult male tahr weighed 123.0% more than adult female tahr (58.3 ± 8.0 vs. 26.2 ± 3.7 kg) (Table 1). Tahr were thus almost five times more sexually size dimorphic than chamois.

Changes in fat mass according to age, sex, and species

In the following, we do not report effect sizes with the p values because slope estimates and their uncertainties are shown on Fig. 1. For male tahr, there was a decline in fat mass during the mating period with increasing age (Fig. 1; Appendix A, Fig. A4). The change in fat mass was much more pronounced between immatures and young adults ($p <$ 0.001) than between young and prime-aged adult males ($p =$ 0.11). The pattern of change in fat mass was weaker for male chamois compared with male tahr (Fig. 1; Appendix A, Fig. A3). There was a similar decline in the fat of immature and young adult male chamois ($p = 0.22$), and the rate of decline of fat tended to increase between young and prime-aged males ($p = 0.06$). Among adult males, the decline in fat mass

was consistently greater in tahr compared with chamois (young adults: $p < 0.001$; prime-aged adults: $p = 0.04$). Fat mass did not change over the mating period in most of the female tahr and chamois age classes (see Fig. 1; Appendix A, Figs. A3 and A4); the decline in the immature female chamois was similar to that recorded for immature male chamois ($p = 0.28$).

Changes in carcass mass according to age, sex, and species

In males, carcass mass declined throughout the mating period for all age and species classes except immature tahr (Fig. 1; Appendix A, Figs. A1 and A2). In both species, there was a lower decline in carcass mass than in fat mass among adult males (in young adult chamois: $p = 0.02$). Changes in carcass mass between species were similar within the immature and young adult male age classes (all $p >$ 0.15), but were greater in prime-aged male tahr than in prime-aged male chamois ($p = 0.005$). In contrast to changes in fat mass, there were no differences in changes in carcass

mass throughout the mating period between young and prime-aged adult males in either tahr ($p = 0.23$) or chamois ($p = 0.42$). As for fat mass, there was no strong pattern of change in the carcass mass of female tahr or chamois during the mating period (Fig. 1; Appendix A, Figs. A1 and A2).

Discussion

We investigated age-related changes in male reproductive effort between two species of polygynous ungulates occupying similar environments (mostly open habitats in mountain terrain) but greatly contrasting in SSD. Our results provide evidence that adult male ungulates of species with large SSD expend more energy during mating than males of species with less SSD, supporting theoretical predictions about the importance of sexual selection in the evolution of SSD (Andersson 1994).

Males and females have contrasting life histories in highly sexually dimorphic ungulates (Clutton-Brock et al. 1982). Males allocate most of their reproductive effort during a short mating period (e.g., red deer: Yoccoz et al. 2002; moose: Mysterud et al. 2005), whereas females do the same during late gestation and early lactation (Sadleir 1969; Clutton-Brock et al. 1989). Accordingly, we did not find any large change in either fat or body masses of adult females in any species during rut, whereas adult males underwent age-dependent decreases in both kidney fat and body masses during the same period (Fig. 1; see also, e.g., reindeer: Leader-Williams and Ricketts 1982; mule deer (*Odocoileus hemionus* (Rafinesque, 1817)): Anderson et al. 1990). Because female ungulates only marginally reduce food intake during rut (Clutton-Brock et al. 1982), variation in female body condition is expected to depend mostly on environmental conditions and the extent of male harassment (fallow deer (*Dama dama* (L., 1758)): Komers et al. 1999; reindeer: Holand et al. 2006). In contrast, consistent declines in the condition of adult male ungulates exhibiting SSD (red deer: Yoccoz et al. 2002; moose: Mysterud et al. 2005; chamois and tahr: this study) are most likely due to a decrease in forage intake (red deer: Bobek et al. 1990; moose: Miquelle 1990; chamois: Willisch and Ingold 2007), and increased energy expenditure associated with reproductive activities (Mysterud et al. 2004). The magnitude of age-related changes of male fat or body masses during rut is expected to vary, as mating tactics change with age (Yoccoz et al. 2002). Indeed, field observations show that young adult males spend less time courting or travelling and more time feeding relative to adult males in both tahr (Forsyth and Tustin 2005) and chamois (Loison 1995).

Sexual selection generates sex-specific differences in resource allocation to growth and reproduction, resulting in the evolution of SSD (Andersson 1994). The main factors affecting the evolution of large body size in males would be the advantages conferred during intra-sexual competition and courtship, such as enhanced or prolonged access to females (Andersson 1994). Loison et al. (1999b) showed that interspecific variation in SSD among ungulates does not depend on interspecific variation in body size, but rather on the species-specific level of polygyny. The difference in SSD between tahr and chamois would thus likely correspond to differences in the intensity of competition among males for access to females. As predicted, our results showed a higher energetic cost of mating in adult male tahr than in adult male chamois (Fig. 1; kidney fat mass), but further studies of their mating tactics and activity budget during rut are needed to assess the importance of male–male sexual competition in these species and to evaluate factors shaping age-dependent variation in energetic costs of mating (see, e.g., fallow deer: McElligott et al. 2003; bighorn sheep: Pelletier 2005; mountain goat (*Oreamnos americanus* (de Blainville, 1816)): Mainguy and Côté 2008). For example, reproductive effort in female ungulates is well known to be affected by body mass (e.g., moose: Garel et al. 2009b), but fewer studies have investigated this relationship in males (e.g., individual quality hypothesis: McElligott et al. 2003). Some studies have suggested that males with more resources at the start of the rut should have greater reproductive effort than other males (e.g., Pelletier 2005; Mainguy and Côté 2008). We may expect such a relationship to be better supported in species showing large SSD because of higher intensity of competition among males than in less dimorphic species.

Our results confirm that as expected for capital breeders, males of tahr and chamois rely on accumulated body reserves to meet the energetic demands of mating. We also found that fat mass decreased at a faster rate than body mass among adult male tahr and chamois. Fat is energy-rich and therefore among the first body tissues to be mobilized (Pond 1998). We suggest that future studies of male reproductive effort using dead animals should measure changes in fat reserves rather than body masses because, although harder to measure, fat appears to be a more sensitive measure of energy expenditure in ungulates than mass (Riney 1955).

Gaining information about the factors shaping variation in reproductive effort will improve our understanding of the relationship between sexual selection and life-history evolution (Stearns 1992). Indeed, variation in the energetic costs of reproduction owing to sex, age, and (or) species (Fig. 1) could lead to fitness costs that should differ depending on the life-history tactic (Hamel et al. 2010). For example, higher energetic costs of reproduction for adult male tahr than for chamois might lead to lower adult survival rates in male tahr compared with chamois (see Loison et al. 1999a; Forsyth et al. 2005).

Acknowledgements

References

Anderson, A.E., Bowden, D.C., and Medin, E. 1990. Indexing the annual fat cycle in a mule deer population. J. Wildl. Manage. **54**(4): 550–556. doi:10.2307/3809348.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Bobek, B., Perzanowski, K., and Weiner, J. 1990. Energy expenditure for reproduction in male red deer. J. Mammal. **71**(2): 230–232. doi:10.2307/1382171.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. 2nd ed. Springer-Verlag, New York.

Byers, J.A., and Waits, L. 2006. Good genes sexual selection in nature. Proc. Natl. Acad. Sci. U.S.A. **103**(44): 16343–16345. doi:10.1073/pnas.0608184103. PMID:17060640.

Caughley, G. 1965. Horn rings and tooth eruption as criteria of age in Himalayan thar, *Hemitragus jemlahicus*. N.Z. J. Sci. **8**: 333–351.

Caughley, G. 1970. Fat reserves of himalayan tahr in New Zealand by season, sex, area and age. N.Z. J. Sci. **13**: 209–219.

Caughley, G. 1971. The season of birth for northern hemisphere ungulates in New Zealand. Mammalia, **35**(2): 204–219. doi:10.1515/mamm.1971.35.2.204.

Clutton-Brock, T.H. 1989. Mammalian mating systems. Proc. R. Soc. Lond. B Biol. Sci. **236**(1285): 339–372. doi:10.1098/rspb.1989.0027. PMID:2567517.

Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1982. Red deer: behaviour and ecology of two sexes. Edinburgh University Press, Edinburgh, U.K.

Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1989. Fitness costs of gestation and lactation in wild mammals. Nature (London), **337**(6204): 260–262. doi:10.1038/337260a0. PMID:2911365.

Clutton-Brock, T.H., Price, O.F., and MacColl, A.D. 1992. Mate retention, harassment, and the evolution of ungulate leks. Behav. Ecol. **3**(3): 234–242. doi:10.1093/beheco/3.3.234.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and evolution of mating systems. Science (Washington, D.C.), **197**(4300): 215–223. doi:10.1126/science.327542. PMID:327542.

Festa-Bianchet, M., Gaillard, J.-M., and Jorgenson, J. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. Am. Nat. **152**(3): 367–379. doi:10.1086/286175. PMID:18811445.

Forsyth, D.M. 2000. Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. J. Zool. (Lond.), **252**(2): 215–225. doi:10.1111/j.1469-7998.2000.tb00616.x.

Forsyth, D.M., and Tustin, K.G. 2005. Himalayan tahr. *In* The handbook of New Zealand mammals. *Edited by* C.M. King. Oxford University Press, Oxford, U.K. pp. 361–373.

Forsyth, D.M., Tustin, K.G., Gaillard, J.-M., and Loison, A. 2004. Fetal sex ratio variation in the highly polygynous Himalayan tahr: evidence for differential male mortality. Behav. Ecol. **15**(4): 572–578. doi:10.1093/beheco/arh063.

Forsyth, D.M., Duncan, R.P., Tustin, K.G., and Gaillard, J.-M. 2005. A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. Ecology, **86**(8): 2154–2163. doi:10.1890/03-0738.

Garel, M., Loison, A., Jullien, J.-M., Dubray, D., Maillard, D., and Gaillard, J.-M. 2009*a*. Sex-specific growth in alpine chamois. J. Mammal. **90**(4): 954–960. doi:10.1644/08-MAMM-A-287.1.

Garel, M., Solberg, E.J., Sæther, B.-E., Grøtan, V., Tufto, J., and Heim, M. 2009*b*. Age, size and spatio-temporal variation in ovulation patterns of a seasonal breeder, the Norwegian moose (*Alces alces*). Am. Nat. **173**(1): 89–104. doi:10.1086/593359. PMID:19072136.

Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Loison, A., Bonenfant, C., and Descamps, S. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecol. Lett. **13**(7): 915–935. doi:10.1111/j.1461-0248.2010.01478.x. PMID:20482573.

Hayssen, V., van Tienhoven, A., and van Tienhoven, A. 1993. Asdell's patterns of mammalian reproduction: a compendium of species-specific data. Cornell University Press, Ithaca, N.Y.

Hewison, A.J.M., and Gaillard, J.-M. 2001. Phenotypic quality and senescence affect different components of reproductive output in roe deer. J. Anim. Ecol. **70**(4): 600–608. doi:10.1046/j.1365-2656.2001.00528.x.

Holand, Ø., Weladji, R.B., Røed, K.H., Gjøstein, H., Kumpula, J., Gaillard, J.-M., Smith, M.E., and Nieminen, M. 2006. Male age structure influences females' mass change during rut in a polygynous ungulate: the reindeer (*Rangifer tarandus*). Behav. Ecol. Sociobiol. **59**(5): 682–688. doi:10.1007/s00265-005-0097-5.

Houssin, H., Loison, A., and Gaillard, J.-M. 1993. Participation à la reproduction des femelles de chamois (*Rupicapra rupicapra*) en fonction de leur âge dans une population alpine chassée. Gibier Faune Sauvage, **10**: 39–45.

Komers, P.E., Birgersson, B., and Ekvall, K. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. Am. Nat. **153**(4): 431–436. doi:10.1086/303185.

Leader-Williams, N., and Ricketts, C. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. Oikos, **38**(1): 27–39. doi:10.2307/3544564.

Loison, A. 1995. Approches intra- et inter-spécifiques de la dynamique des populations : l'exemple du chamois. Ph.D. thesis, Université Claude Bernard Lyon 1, Villeurbanne, France.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., and Jullien, J.-M. 1999*a*. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology, **80**(8): 2539–2554. doi:10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2.

Loison, A., Gaillard, J.-M., Pélabon, C., and Yoccoz, N.G. 1999*b*. What factors shape sexual size dimorphism in ungulates? Evol. Ecol. Res. **1**: 611–633.

Loison, A., Jullien, J.-M., and Menaut, P. 1999*c*. Subpopulation structure and dispersal in two populations of chamois. J. Mammal. **80**(2): 620–632. doi:10.2307/1383306.

Lott, D.F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge, U.K.

Mainguy, J., and Côté, S.D. 2008. Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. Behav. Ecol. Sociobiol. **62**(6): 935–943. doi:10.1007/s00265-007-0517-9.

McElligott, A.G., Naulty, F., Clarke, W.V., and Hayden, T.J. 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? Evol. Ecol. Res. **5**: 1239–1250.

Miquelle, D.G. 1990. Why don't bull moose eat during the rut? Behav. Ecol. Sociobiol. **27**(2): 145–151. doi:10.1007/BF00168458.

Mysterud, A., Yoccoz, N.G., Stenseth, N., and Langvatn, R. 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence.. Proc. R. Soc. Lond. B Biol. Sci. **268**(1470): 911–919. doi:10.1098/rspb.2001.1585.

Mysterud, A., Langvatn, R., and Stenseth, N.C. 2004. Patterns of reproductive effort in male ungulates. J. Zool. (Lond.), **264**(2): 209–215. doi:10.1017/S0952836904005618.

Mysterud, A., Solberg, E.J., and Yoccoz, N.G. 2005. Ageing and reproductive effort in male moose under variable levels of intra-sexual competition. J. Anim. Ecol. **74**(4): 742–754. doi:10.1111/j.1365-2656.2005.00965.x.

Pelletier, F. 2005. Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. Behav. Ecol. **16**(1): 280–285. doi:10.1093/beheco/arh162.

Pelletier, F., Hogg, J.T., and Festa-Bianchet, M. 2006. Male mating effort in a polygynous ungulate. Behav. Ecol. Sociobiol. **60**(5): 645–654. doi:10.1007/s00265-006-0208-y.

Pond, C. 1998. The fats of life. Cambridge University Press, Cambridge, U.K.

R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. N.Z. J. Sci. Tech. **36**: 429–463.

Sadleir, R.M.F.S. 1969. The role of nutrition in the reproduction of wild mammals. J. Reprod. Fertil. **6**(Suppl.): 39–48.

Sand, H. 1998. Costs of reproduction in female moose (*Alces alces*) as measured by means of phenotypic correlations. Can. J. Zool. **76**: 187–193.

Schröder, W., and Von Elsner-Schak, I. 1985. Correct age determination in chamois. *In* The biology and management of mountain ungulates. *Edited by* S. Lovari. Croom Helm, London, U.K. pp. 65–70.

Serrano, E., Alpizar-Jara, R., Morellet, N., and Hewison, A.J.M. 2008. A half a century of measuring ungulate body condition using indices: is it time for a change? Eur. J. Wildl. Res. **54**(4): 675–680. doi:10.1007/s10344-008-0194-7.

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

Weladji, R.B., Mysterud, A., Holand, Ø., and Lenvik, D. 2002. Age-related reproductive effort in reindeer (*Rangifer tarandus*): evidence of senescence. Oecologia (Berl.), **131**(1): 79–82. doi:10.1007/s00442-001-0864-6.

Willisch, C.S., and Ingold, P. 2007. Feeding or resting? The strategy of rutting male alpine chamois. Ethology, **113**(1): 97–104. doi:10.1111/j.1439-0310.2006.01301.x.

Yoccoz, N.G., Mysterud, A., Langvatn, R., and Stenseth, N.C. 2002. Age- and density-dependent reproductive effort in male red deer. Proc. R. Soc. Lond. B Biol. Sci. **269**(1500): 1523–1528. doi:10.1098/rspb.2002.2047. PMID:12184820.

Appendix A

Appendix figures appear on the following pages.

Fig. A1. Changes in the carcass mass (log-transformed) of alpine chamois (*Rupicapra rupicapra*) according to age and sex. Polynomial models (up to the second order) are represented by horizontal lines. Vertical broken lines correspond to the mating period (from 15 November to 14 January) and the vertical solid line to the peak of rut (15 December). Sampling date 1 corresponds to 5 September. Left three panels describe males (M): immatures (1; 0.5 and 1.5 years), young adults (2; 2.5, 3.5, and 4.5 years), and prime-aged adults (3; >4.5 years). Right three panels describe females (F): immatures (1; 0.5 year), young adults (2; 1.5 years), and prime-aged adults (3; >1.5 years).
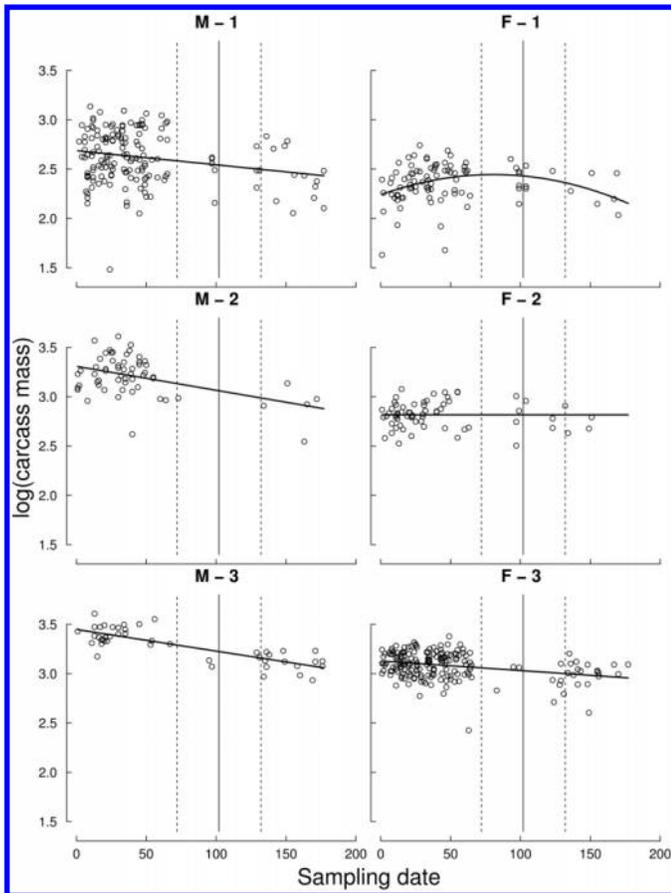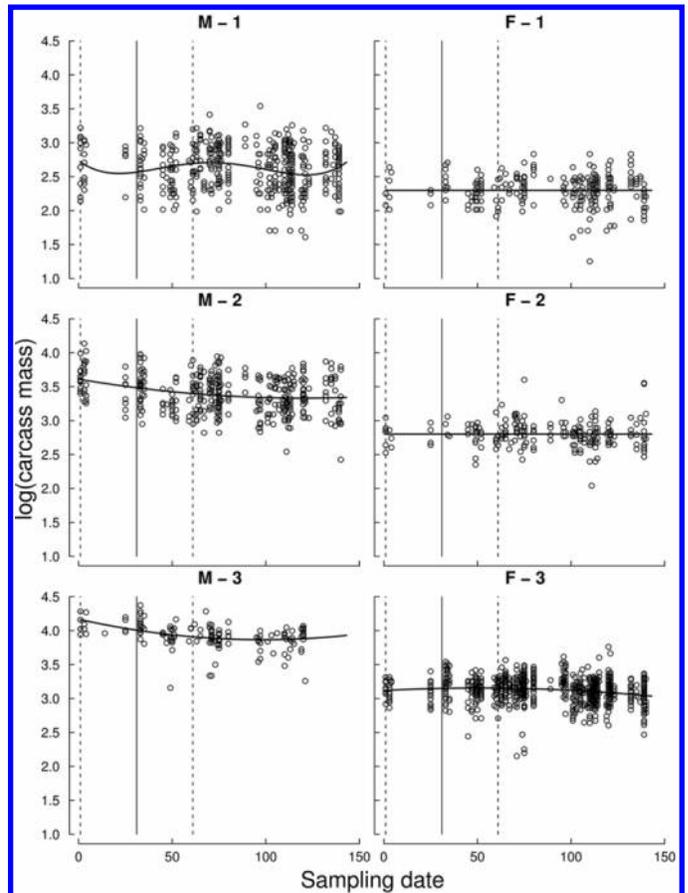
Fig. A2. Changes in the carcass mass (log-transformed) of Himalayan tahr (*Hemitragus jemlahicus*) according to age and sex. Polynomial models (up to the fourth order) are represented by horizontal lines. Vertical broken lines correspond to the mating period (from 5 May to 4 July) and the vertical solid line to the peak of rut (4 June). Sampling date 1 corresponds to 5 May. Left three panels decribe males (M): immatures (1; 0.5 and 1.5 years), young adults (2; 2.5, 3.5, and 4.5 years), and prime-aged adults (3; >4.5 years). Right three panels decribe females (F): immatures (1; 0.5 year), young adults (2; 1.5 years), and prime-aged adults (3; >1.5 years).

Fig. A3. Changes in the kidney fat mass (log-transformed and adjusted for kidney mass; see text for details) of alpine chamois (*Rupicapra rupicapra*) according to age and sex. Polynomial models (up to the third order) are represented by horizontal lines. Vertical broken lines correspond to the mating period (from 15 November to 14 January) and the vertical solid line to the peak of rut (15 December). Sampling date 1 corresponds to 5 September. Left three panels describe males (M): immatures (1; 0.5 and 1.5 years), young adults (2; 2.5, 3.5, and 4.5 years), and prime-aged adults (3; >4.5 years). Right three panels describe females (F): immatures (1; 0.5 year), young adults (2; 1.5 years), and prime-aged adults (3; >1.5 years).
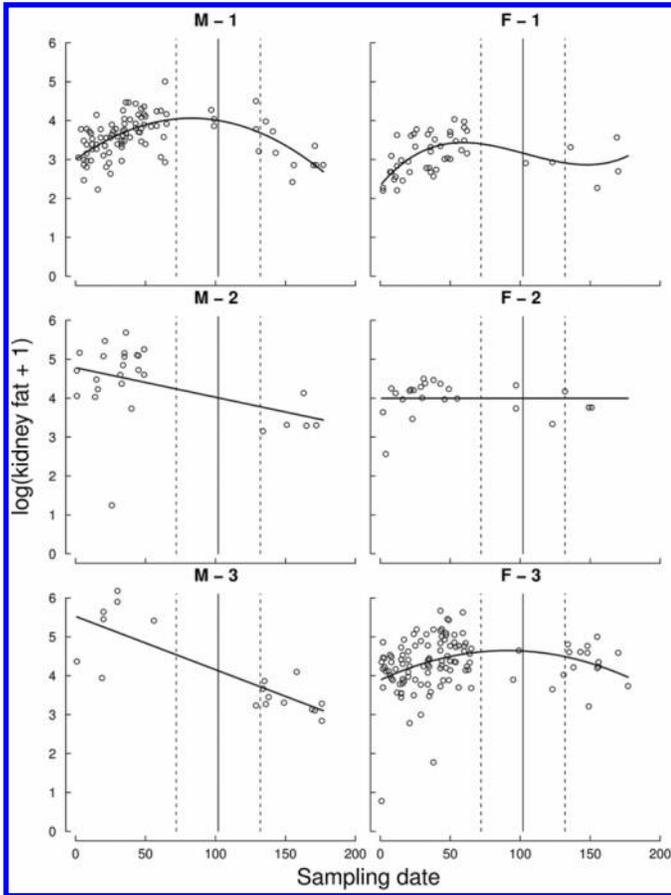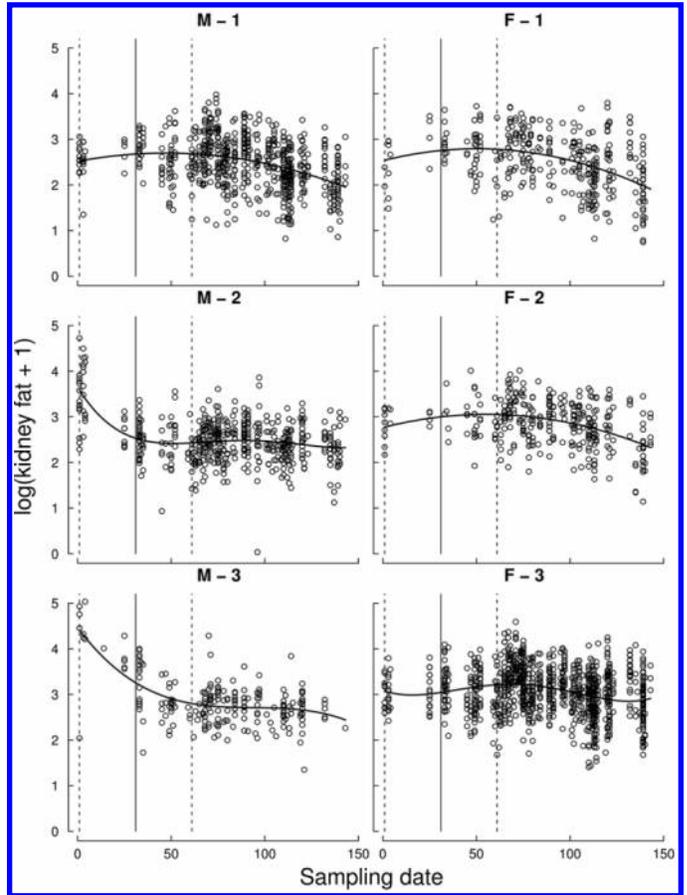
Fig. A4. Changes in the kidney fat mass (log-transformed and adjusted for kidney mass; see text for details) of Himalayan tahr (*Hemitragus jemlahicus*) according to age and sex. Polynomial models (up to the fourth order) are represented by horizontal lines. Vertical broken lines correspond to the mating period (from 5 May to 4 July) and the vertical solid line to the peak of rut (4 June). Sampling date 1 corresponds to 5 May. Left three panels describe males (M): immatures (1; 0.5 and 1.5 years), young adults (2; 2.5, 3.5, and 4.5 years), and prime-aged adults (3; >4.5 years). Right three panels describe females (F): immatures (1; 0.5 year), young adults (2; 1.5 years), and prime-aged adults (3; >1.5 years).