

A SUBSTANTIAL ENERGETIC COST TO MALE REPRODUCTION IN A SEXUALLY DIMORPHIC UNGULATE

DAVID M. FORSYTH,^{1,2,5} RICHARD P. DUNCAN,³ KEN G. TUSTIN,⁴ AND JEAN-MICHEL GAILLARD¹

¹Unite Mixte de Recherche No. 5558, "Biometrie et Biologie Evolutive", Université Claude Bernard Lyon 1, 69622 Villeurbanne Cedex, France

²Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Victoria 3084, Australia

³Bio-Protection and Ecology Division, P.O. Box 84, Lincoln University, Canterbury, New Zealand

⁴2/12 Nile Street, Timaru, New Zealand

Abstract. Whereas the energetic costs of reproduction for female ungulates are well documented, those of males are not. We investigated age- and sex-specific changes in the kidney fat reserves of a large sample of Himalayan tahr (*Hemitragus jemlahicus*), a highly sexually dimorphic and polygynous mountain ungulate, during and following the mating period. Subadult male tahr (2–4 years old) obtain copulations opportunistically by "courting," whereas adult males (>4 years old) spend more time traveling and searching for females, and obtain copulations after engaging in more time-consuming "tending" and "blocking" displays. If there is a cost to these reproductive behaviors, we predicted that (1) the kidney fat index (KFI) of reproductive males (≥ 2 years old) should decline during the mating period relative to females and nonreproductive males, and (2) that the KFI of adult males should decline more than that of subadult males. We formulated our predictions into a series of candidate models, including three covariates also likely to affect fat reserves, and compared support for these models using Akaike's Information Criterion (AIC). The best-fitting model revealed that fat reserves in females and nonreproductive males changed similarly: Fat reserves increased during the mating period, in late autumn and early winter, reached a peak in mid-winter, and then declined throughout the remainder of winter and early spring. In contrast, the fat reserves of reproductive males declined during the mating period, as predicted, and remained low throughout winter. The extent of decline in fat reserves was greater in adult males than in subadult males, also as predicted. Our results strongly imply that male tahr incur a substantial energetic cost for engaging in reproduction and that they trade off reproductive success with reduced body condition during winter, which may lower survival.

Key words: body condition; *Hemitragus jemlahicus*; Himalayan tahr; kidney fat index; reproductive costs; sexual dimorphism; sexual selection; ungulates.

INTRODUCTION

Sexual dimorphism in body mass is a widespread phenomenon among north-temperate ungulates, with males typically growing faster and achieving a greater body mass at maturity than females (Clutton-Brock et al. 1985, Stearns 1992; see for example, red deer, *Cervus elaphus*, Clutton-Brock et al. 1982; and bighorn sheep, *Ovis canadensis*, Festa-Bianchet et al. 1996, Jorgenson et al. 1997). Male reproductive success is most strongly associated with competitive ability, particularly in polygynous species, where larger males have an advantage in acquiring and defending access to females. Sexual size dimorphism is thought to evolve because larger, more competitive males can achieve

greater reproductive success (Andersson 1994, Hogg and Forbes 1997, Coltman et al. 2002).

Long-term studies of marked individuals show that male ungulates typically have lower survival than female ungulates, with male-biased mortality increasing at the onset of reproductive maturity (Gaillard et al. 1993, 2000, Jorgenson et al. 1997, Loison et al. 1999, Töigo and Gaillard 2003). This implies that there may be a substantial cost to male reproduction. Locating and defending access to females may require adult males to invest a lot of time in traveling and courtship/defense behaviors at the expense of feeding, and they may sustain injuries fighting other males (e.g., Clutton-Brock et al. 1982, Bobek et al. 1990, Festa-Bianchet et al. 1990, Hogg and Forbes 1997). The resulting loss of body condition may increase the mortality rate among adult males. Hence, males may trade-off an increase in reproductive success, through locating and maintaining exclusive access to females, with a decline in body condition and a consequently higher rate of mortality.

Manuscript received 5 November 2003; revised 22 August 2004; accepted 11 November 2004; final version received 6 January 2005. Corresponding Editor: M. S. Boyce.

⁵ Present address: Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Victoria 3084 Australia. E-mail: dave.forsyth@dse.vic.gov.au

Whereas the energetic costs of female reproduction (i.e., gestation and lactation) are well documented (e.g., Robbins 1983, Oftedal 1985), few studies have directly documented the costs of male reproduction. Many species of large mammals appear to rely on stored energy for reproduction ("capital breeders"; Stearns 1992, Jönsson 1997, Festa-Bianchet et al. 1998). Doughty and Shine (1997) proposed that the cost of reproductive behaviors in capital breeders should be revealed by changes in energy reserves over the mating period. Indeed, some of the few studies that have attempted to quantify the costs of male reproduction in mammals have adopted this approach. Kojola (1985) reported a higher loss of body mass in prime-aged male reindeer (*Rangifer tarandus*) compared with young males, and Yoccoz et al. (2002) showed that relative loss of body mass in male red deer during the rutting season peaked at prime-age and was lower in younger and senescent males.

In this paper, we examine age- and sex-specific changes in the fat reserves of a large sample of Himalayan tahr (*Hemitragus jemlahicus*), a highly sexually size-dimorphic and polygynous mountain ungulate, during and after the mating period. Fat reserves are a measure of stored energy (Pond 1977). Consequently, we predict that, if there is a cost to male reproduction, the fat reserves of reproductive males should decline during the mating period as they invest energy in reproductive behaviors, whereas the fat reserves of females and nonreproductive males should show a lesser (or no) decline.

Himalayan tahr in New Zealand

Himalayan tahr were introduced into the Southern Alps of New Zealand during 1904–1919 (Caughley 1970a). Tahr established a population at Mt. Cook and subsequently expanded their range both northwards and southwards along the Southern Alps and lateral ranges. Tahr inhabit the shrublands, alpine grasslands, and precipitous rock cliffs between ~750 m and 2250 m in elevation (Forsyth 2000, Forsyth and Tustin, *in press*). By 1976 (the end of our study period), tahr had spread to occupy a range of ~6150 km² (Parkes and Tustin 1985), and reached peak densities of up to 30 tahr/km² (Tustin and Challies 1978) within ~15 years of colonizing an area (Caughley 1970b).

Tahr are extremely sexually dimorphic, with adult males approximately twice the mass of adult females (see *Results*). Males produce sperm (Caughley 1967) and father offspring (Schaller 1977) by 2.5 years of age, but full breeding pelage is not attained until 4.5 years, and males younger than this seldom obtain matings (Schaller 1973, 1977, Forsyth and Tustin, *in press*). Fully reproductive adult males (>4 years of age) attempt to maintain exclusive access to oestrous females by tending and blocking, whereas subadult males (2–4 years) use the alternative mating tactic of coursing (*sensu* Hogg and Forbes 1997). The mating

system of tahr is classified as "tending" (*sensu* Clutton-Brock 1989).

Tahr were initially protected, but concerns about their impacts led to the removal of all protection in 1930. Government-funded hunting began soon after, but apparently had little long-term impact. After 1971, overseas markets for tahr meat were established and helicopters were used by commercial hunters to recover carcasses (Forsyth and Tustin, *in press*).

METHODS

Data collection

Our data came from 4789 Himalayan tahr shot in the Southern Alps of the South Island, New Zealand, during May–September 1972–1976. All tahr were shot by commercial helicopter-based hunters. The helicopter was used as a platform for shooting, and when a group of tahr was encountered as many animals as possible were shot. The animals were eviscerated and ferried by helicopter to the nearest road for transport to a meat-processing factory. Some helicopter crews shot and transported >100 tahr/day (Forsyth and Tustin, *in press*).

Sex was determined by inspection of the external genitalia. The age (in years) was determined for both males and females from the annual growth rings in the right horn (Caughley 1965). Following Riney (1955) and Caughley (1970c), a kidney fat index (KFI) was calculated as 100 × the mass of fat surrounding the kidney (±0.5 g) divided by kidney mass (±0.5 g). To avoid inclusion of mesenteric fat, fat extending beyond the end of the kidney was not weighed (Caughley 1970c). Whether a female was pregnant or not was determined for a small subsample of females that were eviscerated at the roadside (see Forsyth et al. 2004). Because these measurements were made by, or under, the direct supervision of K. G. Tustin, we are confident the data were collected in a consistent manner. Mass was calculated as the eviscerated, hocked, and beheaded carcass minus all bleedable blood (±0.05 kg), and was provided to us by the meat-processing factory from tagged carcasses. The location where each animal was shot was obtained from the helicopter pilot.

Fat is the body component most often associated with body condition (Pond 1977), but measuring the total body fat (TBF) of ungulates is difficult. Riney's KFI is one of the most frequently used indices of fat reserves and of general physical condition. Although the relationship between KFI and TBF has not been investigated for Himalayan tahr in New Zealand, Torbit et al. (1988) showed that KFI was a better index of TBF than another index, femur marrow fat, for mule deer (*Odocoileus hemionus*).

Since ungulates in New Zealand have no predators other than humans, populations are assumed to be food-limited. Caughley (1970b) proposed a four-stage "irruptive" model describing changes in such populations

following colonization of a new area (reviewed in Forsyth, *in press*). The “initial increase” represents the period between establishment and the initial population peak. The “initial stabilization” lasts from the population peak until the start of the decline. The “decline” continues until the population’s exponential rate of increase (r) changes from negative to zero. The “post-decline” is characterized by small fluctuations around an equilibrium density. Riney (1964) suggested that the postdecline density is lower than at the initial peak because the availability of forage has been modified. Caughley (1970a, b, c) tested this model using data from Himalayan tahr in New Zealand. After reconstructing the range expansion of tahr, Caughley selected one sampling site to represent each of the four hypothesized stages, and shot between 72 and 1090 tahr at each site during November–February 1964–1965. Caughley (1970b) predicted that fat reserves should be highest for the initial increase, lowest for the decline, and “somewhere between” for the initial stabilization and postdecline populations. Comparisons of the KFI of females >1 year old supported his model (Caughley 1970b). Furthermore, time since colonization, population density and r were found to be related in the manner expected. In the population sampled ~10 years after colonization (initial increase stage), r was 0.13, whereas in the population sampled ~20 years after colonization (initial stabilization stage), r was close to 0 (Caughley 1970b). Since the abundance of preferred food species was also shown to decline with time since colonization, it was concluded that these demographic changes were driven by depletion of the food resource (Caughley 1970b).

The tahr in this study were sampled from 18 areas (Appendix A), including all of the catchments sampled in 1964–1965 by Caughley (1967, 1970a, b, c). We used the detailed history of colonization described in Caughley (1970a) and Parkes and Tustin (1985) to classify the 18 catchments according to the period in which female tahr colonized the area (male tahr often preceded the arrival of females by many years; Caughley 1970a). Parkes and Tustin (1985) reconstructed the distribution of female tahr in the Southern Alps in 1936, 1946, 1956, 1966, and 1976. We identified the interval in which each of the 18 areas was colonized. Using the midpoints of these intervals (assuming that areas colonized by 1936 were colonized in 1931, a reasonable assumption given the relatively slow initial range expansion of tahr from Mt. Cook [Caughley 1970a]), and subtracting these midpoints from the year of first sampling (1972), gives the approximate number of years since colonization as either 11, 21, 31, or 41 years.

Model development and analysis

Our main aim was to test the prediction that, if males are investing energy into reproductive behaviors (at the expense of feeding) to maximize their reproductive success, the fat reserves of reproductive males should

decline during the mating period relative to females and nonreproductive males. Furthermore, a cost to male reproduction should also be evident as differences among reproductive males. Adult males (>4 years old) that engage in more time-consuming reproductive behaviors should exhibit a greater decline in fat reserves than subadult males (2–4 years old).

Our study included data on the fat reserves (KFI) of tahr shot at different times in the period 5 May–23 September in each of five years (1972–1976). The period of sampling in each year includes the mating period (May to mid-July; Forsyth and Tustin, *in press*), winter (June–August), and early spring (September). Throughout the mating period, reproductive males mingle with groups of females and compete with each other for matings. Adult males (>4 years old) will remain with a female group when there is a female in estrous, and attempt to maintain exclusive access to that female by tending and blocking (sensu Hogg and Forbes 1997). Tending involves an adult male displaying to a female by facing her at right angles, with head and muzzle held high and mane erect; this pose can be maintained for >5 hours. The courtship display intensifies with a “head nod” and the tongue extended or flicked, leading finally to copulation. Blocking behavior involves display contests between adult males. These displays can last for up to an hour, but rarely result in fighting (Schaller 1977, Forsyth and Tustin, *in press*). When it does occur, fighting involves a head-to-head wrestle, with both pushing until one loses balance so that the victor can swipe his horns (which can be up to 400 mm long) at the loser’s body (Forsyth and Tustin, *in press*).

Adult males spend more time traveling and searching for females than subadult males (2–4 years old; K. G. Tustin, *unpublished data*). Subadult males typically stay with one female group throughout the winter, and obtain opportunistic matings by courting (sensu Hogg and Forbes 1997). This involves one or more subadult males chasing a female until she is cornered and can be forcibly copulated. However, relative to adult males, subadults spend less time engaging in reproductive behavior (Forsyth and Tustin, *in press*). Copulations by males <2 years of age have not been observed (Schaller 1977, Forsyth and Tustin, *in press*).

Both adult and subadult males feed little during the mating period. Females and nonreproductive males feed until deep snow restricts all animals to snow-free bluffs at high altitude (Forsyth 2000), after which feeding and other movement is minimized (Tustin and Parkes 1988, Forsyth and Tustin, *in press*). July and August are generally the months of coldest temperatures and greatest snow cover when feeding and movement are most restricted. When the snows melt in spring (beginning in September), tahr descend to low altitudes to feed on the flush of new growth (Tustin and Parkes 1988). At this time, adult and subadult males form separate groups and move to grassland and shrubland habitats away from groups of females and

TABLE 1. The seven candidate models for explaining variation in log-transformed values of kidney fat index (KFI) of 3284 Himalayan tahr.

Model	Age–sex classes	Simplified model	AIC
1	None	$SD^4 + YS + Col + Cohort$	6325.6
2	Male	$SD^4 + Class + Class \times SD^3 + YS + Col + Cohort$	5548.2
	Female		
3	Male 0–1, >1	$SD^4 + Class + Class \times SD^3 + YS + Col + Cohort$	5290.8
	Female		
4	Male 0–1, >1	$SD^4 + Class + Class \times SD^3 + YS + Col + Cohort$	5274.9
	Female 0–1, >1		
5	Male 0–1, 2–4, >4	$SD^4 + Class + Class \times SD^3 + YS + Col + Cohort$	5253.2
	Female 0–1, >1		
6	Male 0–1, 2–4, >4	$SD^4 + Class + Class \times SD^4 + YS + Col + Cohort$	5256.3
	Female 0–1, 2–4, >4		
7	Male 0–1, 2–4, 5–8, >8	$SD^4 + Class + Class \times SD^3 + YS + Col + Cohort$	5258.1
	Female 0–1, >1		

Notes: SD^n refers to the variable sampling date (with 5 May as day 1) and its polynomial terms up to the n th order, and likewise for the interaction terms $Class \times SD^n$. AIC is the value of Akaike's Information Criterion for each of the simplified models. Abbreviations are: YS, year shot; and Col, year colonized. The best-fit model (lowest AIC value) is highlighted in boldface type.

nonreproductive males (Forsyth 1999, 2000, Forsyth and Tustin, *in press*). Pregnant females give birth to a single kid, with the median birth date in New Zealand being 30 November ($SD = 18.5$ d; Caughley 1971).

Some data on seasonal changes in KFI for tahr in New Zealand have been published (Caughley 1970c). That work was based on a much smaller sample than available here. Caughley (1970c) showed that the kidney fat reserves of females reached a minima in summer, increased through autumn to a maxima in early winter, and then declined from late winter to summer. Males followed a similar pattern except that peak kidney fat reserves were recorded earlier in the year in progressively older age classes. Caughley suggested that this reflected a physiological shift from the “female” pattern to a “breeding male” condition.

We defined the first sampling day in this study (5 May) as day 1, with sampling continuing up to day 142 (23 September) in each year. Given our hypothesis and knowledge of tahr biology, we predicted that females and nonreproductive males should show similar changes in kidney fat reserves throughout the sampling period, with KFI increasing through late autumn and early winter (including the mating period) to reach a peak in winter and then decline (Caughley 1970c). In contrast, we predicted that the kidney fat reserves of reproductive males should decline during the late autumn/early winter mating period, as energy is expended in reproductive behaviors at the expense of feeding, and that this decline should be greater in adult (>4 years) than subadult (2–4 year) males.

These predictions translate into a model in which the response variable (KFI) should be a nonlinear function of sampling date (i.e., day 1–142), with the form of the function differing among age–sex classes. We defined two female age classes based on the proportion of females pregnant (Forsyth et al. 2004). Only 12% of the 951 females shot aged 0–1 year were pregnant, so this class was termed nonreproductive females. In

contrast, 88% of the 1695 females shot aged >1 years were pregnant and this class was termed reproductive females. Three male age classes were defined based upon the production of sperm (Caughley 1967), body mass (see the following paragraphs) and reproductive behavior (Forsyth and Tustin, *in press*). Nonreproductive males (0–1 year) do not produce sperm, have a small mass, and have not been observed engaging in reproductive behavior. Subadult (2–4 years) males produce sperm, have moderate mass, and engage in courting, but not prolonged tending and blocking behavior. Adult males (>4 years) have large mass and engage primarily in tending and blocking behavior. Sample sizes for the age–sex classes are given in Appendix B.

To determine how the relationship between KFI (log-transformed) and sampling date differed between age–sex classes, we compared seven candidate models in which the age–sex classes were defined in different ways (Table 1). In addition to the age–sex classes described in the previous paragraph, two of the models included additional classes: females >4 years and males >8 years old, with the aim of determining if the form of the relationship between KFI and sampling date changes in older animals. By identifying which of the candidate models best describes the data, we can establish how the relationship between KFI and sampling date differs between age–sex classes and whether these differences match our predictions.

To capture the expected nonlinear relationships between KFI and sampling date, each model included sampling date along with its polynomial terms up to the fifth order as both main effects and in interactions with age–sex class. In addition to the effects of sampling date and age–sex class, we also included three covariates likely to influence KFI. First, mean KFI was likely to differ from year to year due to interannual variation in the availability and quality of forage (e.g., Post and Stenseth 1999). We accounted for this by including the categorical variable “year shot” in each

model. Second, animals born in good or poor years may differ in their initial body condition and carry that effect through their lifetime, termed “cohort variation” (e.g., Gaillard et al. 1997, 2000). We therefore included the categorical variable “cohort” (the year in which animals were born) in each model. Third, animals were shot from areas that had been colonized at different times and that consequently supported tahr populations at different densities and different stages following colonization. Following Caughley (1970*b*), we expected mean KFI to be lower in areas of high density (those colonized 21 and 31 years ago) relative to areas of low density (those colonized 11 and 41 years ago). To account for this, we included the categorical variable “year colonized” in each model.

Each of the candidate models was simplified using backward selection, removing any nonsignificant terms ($P < 0.05$ based on F tests) beginning with the highest order polynomial interaction terms, followed by the highest order polynomial terms and any other nonsignificant main effects. The resulting “simplified” models describe how KFI varies with the three covariates and sampling date for the age–sex classes defined in each model.

We used Akaike’s Information Criterion (AIC) to identify which of these seven models best fitted the data (Burnham and Anderson 2002). The best-fitting model has the smallest AIC value, and we ranked models from best to worst based on the difference between each model’s AIC and the AIC of the best-fitting model (Δi values). We also calculated the Akaike weights (w_i ; see Burnham and Anderson 2002); these provide an approximate probability that the best-fitting model is in fact the best out of the candidate set. The results of the model selection process are presented following the recommendations of Anderson and Burnham (2002).

We used the statistical package R, version 1.7.0 (The R Development Core Team 2003), to fit the models to the data and to obtain AIC values, estimates of model parameters, and standard errors of the parameter estimates.

RESULTS

Sex–ratio and sexual size dimorphism

Male tahr comprised a slightly greater proportion of the sample population than female tahr for ages 0–2 years (Fig. 1). For animals three years and older, there was a progressive decline in the proportion of males relative to females, such that for animals 10 years of age and older, males comprised only 11% of the sample. The oldest male and female sampled were 14 and 19 years, respectively.

Although males aged 0 and 1 year were slightly heavier than females, sex differences in mass became more apparent at two years (Fig. 1). After two years, the mass of females increased relatively little. In contrast, males continued to increase in mass, attaining



FIG. 1. The sex ratio (open squares) and masses (mean \pm SE) of male (open circles) and female (solid circles) Himalayan tahr by age. Note that age class 10 includes animals 10 years and older (total sample sizes: $n = 2143$ males, and $n = 2646$ females).

average adult male mass by six years. For animals ≥ 6 years, the mean male mass of 52.3 ± 0.82 kg (mean \pm SE) was 2.1 times greater than the average female mass of 24.9 ± 0.19 kg.

Changes in KFI with sampling date and age–sex class

A model grouping animals into five age–sex classes (reproductive and nonreproductive females, and nonreproductive, subadult, and adult males) provided the best fit to the data with probability >0.7 (model 5 in Table 1 and Appendix C). Two other models (6 and 7) received some support, with Δi values of 3–5. These models differed from the best-fit model by including an additional age–sex class (either females >4 years or males >8 years). However, there was very little difference in the shape of the relationships between KFI and sampling date in these older age–sex classes relative to the shape obtained when these classes were subsumed in the best-fit model. Consequently, model 5 provided the best description of the data, and our findings would have been the same had we selected either models 6 or 7. The remaining models received virtually no support.

Females and nonreproductive males (0–1 year) showed a similar pattern of change in fat reserves with sampling date (Figs. 2 and 3). KFI generally increased through late autumn and early winter to reach a peak in mid July, and then declined throughout the remainder of winter and into spring. In contrast, reproductive males showed a very different pattern. Subadult males (2–4 years) started with similar fat reserves to reproductive females in early May, but KFI declined throughout late autumn to reach a trough in early winter and then remained low throughout winter and spring. Adult males (>4 years) started with the highest fat reserves in early May, but these declined throughout late autumn and early winter to reach a trough in late July–August, before increasing slightly in spring.

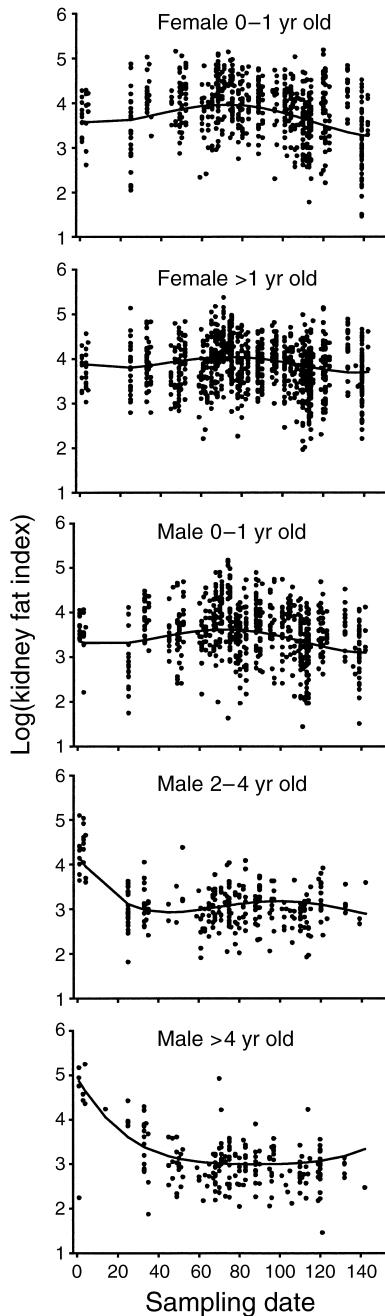


FIG. 2. Scatter plots of log-transformed values of kidney fat index (KFI) by sampling date for the age–sex classes of Himalayan tahr identified as differing in the best-fit model, along with the expected values of log(KFI) obtained from that model (see Table 2). Day 1 is 5 May. The lines are the expected values of log(KFI) from the best-fit model (Table 2) keeping year shot, year colonized, and cohort constant at the values for 1975, 11, and 1971, respectively.

Mean KFI varied with year shot, number of years since colonization, and cohort. As predicted, mean KFI was higher in areas that had been colonized for the longest (41-year) and shortest (11-year) period, where tahr densities were predicted to be low (Table 2).

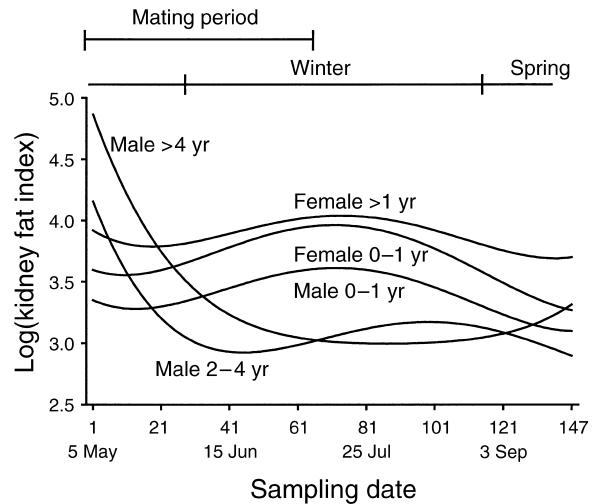


FIG. 3. Expected values of log-transformed kidney fat index (KFI) for age–sex classes from the best-fit model (see Table 2) keeping the covariates year shot, year colonized, and cohort constant at the values for 1975, 11, and 1971, respectively.

DISCUSSION

Our results support the hypothesis that there is a substantial energetic cost to male reproduction in Himalayan tahr. The best-fit model shows that the relationship between fat reserves and sampling date varies with age–sex class such that reproductive and nonreproductive females and nonreproductive, subadult, and adult males differ. These changes in fat reserves follow two distinct patterns. The fat reserves of females and nonreproductive males increase during the mating period and then decline during late winter. In contrast, the fat reserves of reproductive males decline during the mating period and remain low throughout winter (Fig. 3). The most likely explanation for the decline in fat reserves in males during the mating season, when nonreproductive male and female fat reserves are increasing, is that during this period males invest a substantial amount of time in reproductive behaviors at the expense of feeding, thereby reducing the ratio of energy gain to requirements (*sensu* Parker et al. 1999).

Adult males (>4 years) entered the mating period with substantially higher mean fat reserves than subadult males (2–4 years). Despite this, fat reserves in both classes declined to similar low values during winter. This more marked decline in the fat reserves of adult males during the mating period matches our prediction based on differences in the reproductive behavior of these two age classes. Adult males of similar size compete for females with ritualized contest displays and spend substantial amounts of time courting reproductive females (Schaller 1973, 1977, Forsyth and Tustin, *in press*); these extended displays are at the cost of feeding (see Maher and Byers 1987, Miquelle 1990). Relative to adult male tahr, subadult males spend less

TABLE 2. Parameter estimates and standard errors for the best-fitting model (Model 5 in Table 1 and Appendix C) explaining variation in the log-transformed values of kidney fat index (KFI) for 3284 Himalayan tahr.

Parameter	Estimate	SE
Intercept	2.513	0.5526
Sampling date	-0.01081	0.007639
Sampling date ²	0.0006273	0.0001731
Sampling date ³	-0.000007602	0.000001613
Sampling date ⁴	0.00000002486	0.00000005315
Female _{0-1 yr}	0	
Female _{>1 yr}	0.3298	0.1702
Male _{0-1 yr}	-0.2436	0.1658
Male _{2-4 yr}	0.6214	0.1642
Male _{>4 yr}	1.335	0.2385
Sampling date × Female _{0-1 yr}	0	
Sampling date × Female _{>1 yr}	-0.007586	0.007686
Sampling date × Male _{0-1 yr}	-0.002901	0.008118
Sampling date × Male _{2-4 yr}	-0.06343	0.008420
Sampling date × Male _{>4 yr}	-0.06838	0.01213
Sampling date ² × Female _{0-1 yr}	0	
Sampling date ² × Female _{>1 yr}	0.00005371	0.0001138
Sampling date ² × Male _{0-1 yr}	0.00001493	0.0001224
Sampling date ² × Male _{2-4 yr}	0.0007822	0.0001331
Sampling date ² × Male _{>4 yr}	0.0006004	0.0001966
Sampling date ³ × Female _{0-1 yr}	0	
Sampling date ³ × Female _{>1 yr}	0.0000003713	0.0000005005
Sampling date ³ × Male _{0-1 yr}	0.0000006624	0.0000005434
Sampling date ³ × Male _{2-4 yr}	-0.000002711	0.0000006134
Sampling date ³ × Male _{>4 yr}	-0.000001279	0.0000009368
Year shot ₁₉₇₂	0	
Year shot ₁₉₇₃	0.1557	0.03765
Year shot ₁₉₇₄	-0.02524	0.04200
Year shot ₁₉₇₅	-0.1286	0.04312
Year shot ₁₉₇₆	-0.1147	0.07639
Colonized ₁₁	0	
Colonized ₂₁	-0.1307	0.02911
Colonized ₃₁	-0.1691	0.03175
Colonized ₄₁	-0.02031	0.05005
Cohort ₁₉₇₁	1.222	0.5377

Notes: This model explained 34% of the total variation. Only the parameter estimate for the 1971 cohort (which was used in constructing Figs. 2 and 3) is shown.

time searching for females and engaging in reproductive behavior (Forsyth and Tustin, *in press*). Although several studies have claimed that the major cost of reproduction for male ungulates originates from fighting with other males (e.g., Alvarez 1993, Komers et al. 1994), declining fat reserves in male Himalayan tahr result primarily from substituting feeding with mate finding and courtship behaviors. Nevertheless, the greatest decline in KFI for both subadult and adult males occurred in the first 20 days of sampling (Fig. 2), which is prior to the main period of mating. Reproductive males may engage in costly intra-sexual behaviors prior to mating or may invest in costly travel from their summer to winter ranges in that period (Forsyth 1999, 2000). A study of individual behavior is required to determine which activities contribute to change in body condition prior to and during the mating period.

Yoccoz et al. (2002) observed a greater relative decline in the mass of prime-aged males relative to younger and senescent males in red deer, but we found little support for such a pattern for body condition in Himalayan tahr. The pattern of change in fat reserves with

sampling date did not differ substantially in older (>8 years) relative to younger (4–8 years) adult males.

In contrast to reproductive males, females and non-reproductive males increased their fat reserves through the mating period, with peak reserves coinciding with the winter period when snow starts to restrict movement and feeding, and animals become confined to rocky outcrops (Tustin and Parkes 1988). The declines in fat reserves after mid-winter are presumably due to snow cover restricting movement and limiting forage availability. For pregnant females, the decline in fat reserves could also result from diverting stored energy to the developing fetus (Robbins 1983, Oftedal 1985), although there was no indication that the fat reserves of reproductive females (>1 year) declined more than those of nonreproductive females (0–1 year; Fig. 3).

Overall, the two distinct patterns of change in fat reserves for reproductive males vs. females and non-reproductive males represent two different energy investment strategies. To maximize their reproductive success, males accumulate fat reserves prior to the mating period and then deplete those reserves during the mating period, investing energy in gaining and main-

taining access to females. As a consequence, males enter the winter with very low reserves. In contrast, females and nonreproductive males accumulate fat reserves during the mating period. These fat reserves peak in mid-winter but then decline when the ratio of energy requirement to energy gain must be at its highest (Mautz 1978, Parker et al. 1996, 1999).

There are no mark-recapture data with which to estimate age-sex specific survival rates in Himalayan tahr populations, and no study has directly linked low winter fat reserves with an increased probability of mortality. Nevertheless, our results are consistent with the hypothesis that low winter fat reserves in reproductive-aged male tahr, resulting from energy investment during the mating period, lead to higher rates of mortality and an increasingly female-biased sex ratio with age (Fig. 1; see Loison et al. 1999). Among north-temperate ungulates in general, most non-hunting adult mortality occurs in winter following the breeding season (e.g., Whitlaw et al. 1998, Ditchkoff et al. 2001, DelGiudice et al. 2002). Ditchkoff et al. (2001) showed that male white-tailed deer ≥ 3.5 years of age were more susceptible to natural mortality than younger adults, and that death "usually followed the breeding season." Overwinter changes in body condition, of which fat reserves are a major component, must be an important determinant of survival. In Himalayan tahr, the timing of the shift toward a female-biased sex ratio (at two years of age, see Fig. 1) coincides with the onset of male reproductive behavior, and the shift in males from a "female" to a "male" pattern of seasonal energy investment (Fig. 3). Hence, at the onset of male reproductive maturity, the period when fat reserves are at their lowest shifts from summer (Caughley 1970*b, c*) to winter, when energy requirements for survival are at their highest.

The ideal method for estimating the costs of reproduction in male mammals would be to measure the behavior, energetics, and condition of individuals multiple times during the mating period. However, such an approach is difficult for wild animals. Our comparison of individuals shot at different times during the mating period did not consider three processes likely to affect KFI. First, individuals may have commenced mating at different times as a function of their condition (McElligott et al. 2003). Second, mating may have commenced at different times in different years (McElligott et al. 2003). Third, same-age males may have exhibited different mating strategies that may have had different energetic costs (Moore et al. 1995, Hogg and Forbes 1997). These processes would explain some of the unexplained variation in KFI. Hence, it is likely that the true costs of reproduction for male tahr are greater than estimated here.

Influence of colonization, year shot, and cohort on fat reserves

Our results, using a much larger sample from many "replicates" of colonization history (see Appendix A),

confirm the earlier findings of Caughley (1970*b, c*). He predicted that the KFI of adult female tahr would be highest in populations during the initial increase stage of colonization, lower during the initial stabilization stage, lower still during the decline stage, and high again in the postdecline stage. Caughley's prediction was based on hypothesized positive relationships between KFI and both survival and reproductive rates, with the latter two variables determining changes in the rate of increase during the four stages of the irruption (see *Methods*). We observed this U-shaped relationship between fat reserves and timing of colonization (Table 2). Animals in sites colonized for the shortest (11 years) and longest (41 years) time had higher mean fat reserves than those colonized at intermediate times (21 and 31 years), adding further support to Caughley's irruptive model of population dynamics for large herbivores.

Year shot also explained variation in fat reserves, with animals shot in 1973 having higher mean fat reserves than animals shot in other years. Climatic conditions in the period prior to harvest are likely to affect fat reserves both directly and indirectly. Temperature and precipitation will directly affect fat reserves through thermoregulatory requirements (Parker et al. 1996, 1999), and indirectly through its effects on the quality and quantity of forage available to animals in the previous and current seasons (e.g., Post and Stenseth 1999).

Cohort was also an important predictor of the body condition of tahr. Hence, conditions during the first year of life had delayed effects on the subsequent condition of individuals. This long-term "quality effect" has previously been shown to be important for both body mass and survival in ungulates (review in Gaillard et al. 2000).

CONCLUSION

Although the energetic costs of reproduction in female ungulates are well known, this is the first study to investigate the costs of male reproduction in terms of energy investment as measured by changes in body fat reserves. Our results show that male Himalayan tahr incur a substantial energetic cost during the mating period, presumably from engaging in reproductive behaviors at the expense of feeding, and that this cost is higher for reproductive adult males than for reproductive subadult males. The age at which an energetic cost to male reproduction is apparent coincides with the onset of male reproductive maturity and a shift in the population sex ratio toward a female bias. Energy invested during the mating period leaves reproductive males with low fat reserves during winter, which is likely to explain their apparently high rates of mortality. Hence, our results strongly imply that males trade-off increased reproductive success, through energy investment during the mating period, with reduced body condition and lower survival during winter.

ACKNOWLEDGMENTS

We thank the helicopter pilots (N. Boyd, M. Cain, N. Cox, B. Winefield, E. McGregor, R. Ellwood, K. Neylon, J. Wilson, T. Jones, and A. Cauldwell) and their crews for their generous assistance in accessing carcasses for necropsy, and J. Morrisey and staff at Edmonds Game Packing Factory for recording the body mass of carcasses. New Zealand Forest Service Ranger M. Barnett helped with liaison, and Forest Range and Experiment Station staff R. Lyes, A. Richards, B. Hall, and K. Dillon helped collect data. The senior author acknowledges the support of the CNRS during the preparation of this manuscript. A. Wanrooy drew Appendix A. Comments by M. Festa-Bianchet, T. Coulson, A. Loison, and M. Boyce improved this manuscript.

LITERATURE CITED

- Alvarez, F. 1993. Risks of fighting in relation to age and territory holding in fallow deer. *Canadian Journal of Zoology* **71**:376–383.
- Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* **66**:912–918.
- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.
- Bobek, B., K. Perzanowski, and J. Weiner. 1990. Energy expenditure for reproduction in male red deer. *Journal of Mammalogy* **71**:230–232.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Caughley, G. 1965. Horn rings and tooth eruption as criteria of age in the Himalayan tahr, *Hemitragus jemlahicus*. *New Zealand Journal of Science* **8**:333–351.
- Caughley, G. 1967. Growth, stabilisation and decline of New Zealand populations of the Himalayan tahr (*Hemitragus jemlahicus*). Dissertation. University of Canterbury, Christchurch, New Zealand.
- Caughley, G. 1970a. Liberation, dispersal and distribution of Himalayan tahr (*Hemitragus jemlahicus*) in New Zealand. *New Zealand Journal of Science* **13**:220–239.
- Caughley, G. 1970b. Eruption of ungulate populations, with emphasis on Himalayan tahr in New Zealand. *Ecology* **51**:53–72.
- Caughley, G. 1970c. Fat reserves of Himalayan tahr in New Zealand by season, sex, area and age. *New Zealand Journal of Science* **13**:209–219.
- Caughley, G. 1971. The season of births for Northern Hemisphere ungulates in New Zealand. *Mammalia* **35**:204–219.
- Clutton-Brock, T. H. 1989. Mammalian mating tactics. *Proceedings of the Royal Society of London, Series B* **236**:339–372.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**:131–133.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behaviour and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.
- Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London, Series B* **269**:165–172.
- DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* **66**:698–717.
- Ditchkoff, S. S., E. R. Welch, Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among male white-tailed deer support mate-competition theory. *Journal of Wildlife Management* **65**:552–559.
- Doughty, P., and R. Shine. 1997. Detecting life-history trade-offs: measuring energy stores in “capital” breeders reveals costs of reproduction. *Oecologia* **110**:508–513.
- Festa-Bianchet, M., M. Apollonio, F. Mari, and G. Rasola. 1990. Aggression among lekking male fallow deer: territory effects and relationship with copulatory success. *Ethology* **85**:236–246.
- Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* **152**:367–379.
- Festa-Bianchet, M., J. T. Jorgenson, W. J. King, K. G. Smith, W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. *Canadian Journal of Zoology* **76**:330–342.
- Forsyth, D. M. 1999. Long-term harvesting and male migration in a New Zealand population of Himalayan tahr *Hemitragus jemlahicus*. *Journal of Applied Ecology* **36**:351–362.
- 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. *Journal of Zoology (London)* **252**:215–225.
- Forsyth, D. M. *In press*. Controls on the population dynamics of invading mammals. In W. G. Lee and R. Allen, editors. *Biological invasions in New Zealand*. Springer-Verlag, Berlin, Germany.
- Forsyth, D. M., and K. G. Tustin. *In press*. Himalayan tahr. In C. M. King, editor. *The handbook of New Zealand mammals*. Second edition. Oxford University Press, Auckland, New Zealand.
- Forsyth, D. M., K. G. Tustin, J.-M. Gaillard, and A. Loison. 2004. Fetal sex ratio variation in the highly polygynous Himalayan tahr: evidence for differential male mortality. *Behavioral Ecology* **15**:572–578.
- Gaillard, J.-M., J.-M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J.-D. Lebreton. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**:502–513.
- Gaillard, J.-M., D. Delorme, J. M. Boutin, G. V. Laere, B. Boisubert, and R. Pradel. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. *Journal of Animal Ecology* **62**:778–791.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Tôigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367–393.
- Hogg, J. T., and S. H. Forbes. 1997. Mating in bighorn sheep: frequent male reproduction via a high risk “unconventional” tactic. *Behavioral Ecology and Sociobiology* **41**:33–48.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**:57–66.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease and density on survival of bighorn sheep. *Ecology* **78**:1019–1032.
- Kojola, I. 1985. Influence of age on the reproductive effort of male reindeer. *Journal of Mammalogy* **72**:208–210.
- Komers, P. E., F. Messier, and C. C. Gates. 1994. Plasticity of reproductive behaviour in wood bison bulls: on risks and opportunities. *Ethology, Ecology and Evolution* **6**:485–495.
- Loison, A., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and J.-M. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* **80**:2539–2554.
- Maher, C. R., and J. A. Byers. 1987. Age-related changes in reproductive effort of male bison. *Behavioral Ecology and Sociobiology* **21**:91–96.

- Mautz, W. W. 1978. Sledding on a brushy hillside: the fat cycle in deer. *Wildlife Society Bulletin* **6**:88–90.
- McElligott, A. G., F. Naulty, W. V. Clarke, and T. J. Hayden. 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evolutionary Ecology Research* **5**:1239–1250.
- Miquelle, D. G. 1990. Why don't bull moose east during the rut? *Behavioral Ecology and Sociobiology* **27**:145–151.
- Moore, N. P., P. F. Kelly, J. P. Cahill, and T. J. Hayden. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology* **36**:91–100.
- Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215–238 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Canadian Journal of Zoology* **74**:442–450.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildlife Monographs* **142**:1–48.
- Parke, J. P., and K. G. Tustin. 1985. A reappraisal of the distribution and dispersal of female Himalayan thar in New Zealand. *New Zealand Journal of Ecology* **8**:5–10.
- Pond, C. M. 1977. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annual Review of Ecology and Systematics* **9**:519–570.
- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**:1322–1339.
- R Development Core Team. 2003. The R environment for statistical computing and graphics. Version 1.7.0. (<http://www.r-project.org>)
- Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. *New Zealand Journal of Science and Technology* **36**:429–463.
- Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. *IUCN Publications New Series* **4**:261–273.
- Robbins, C. T. 1983. *Wildlife feeding and nutrition*. Academic Press, London, United Kingdom.
- Schaller, G. B. 1973. Observations on Himalayan tahr (*Hemitragus jemlahicus*). *Journal of the Bombay Natural History Society* **70**:1–24.
- Schaller, G. B. 1977. *Mountain monarchs*. University of Chicago Press, Chicago, Illinois, USA.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Töigo, C., and J.-M. Gaillard. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environmental harshness? *Oikos* **101**:376–384.
- Torbit, S. C., L. H. Carpenter, R. M. Bartmann, A. W. Alldredge, and G. C. White. 1988. Calibration of carcass fat indices in wintering mule deer. *Journal of Wildlife Management* **52**:582–588.
- Tustin, K. G., and C. N. Challies. 1978. The effects of hunting on the numbers and group sizes of Himalayan thar (*Hemitragus jemlahicus*) in Carneys Creek, Rangitata catchment. *New Zealand Journal of Ecology* **1**:153–157.
- Tustin, K. G., and J. P. Parke. 1988. Daily movement and activity of female and juvenile Himalayan thar (*Hemitragus jemlahicus*) in the eastern Southern Alps. *New Zealand Journal of Ecology* **11**:51–59.
- Whitlaw, H. A., W. B. Ballard, D. L. Sabine, S. J. Young, R. A. Jenkins, and G. J. Forbes. 1998. Survival and cause-specific mortality rates of adult white-tailed deer in New Brunswick. *Journal of Wildlife Management* **62**:1335–1341.
- Yoccoz, N. G., A. Mysterud, R. Langvatn, and N. C. Stenseth. 2002. Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society of London, Series B* **269**:1523–1528.

APPENDIX A

A figure showing the 18 areas where 4789 Himalayan tahr were shot during May–September, 1972–1976, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-114-A1.

APPENDIX B

A table showing the number of Himalayan tahr included in this study by age–sex class, and the number for which kidney fat index (KFI) was measured, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-114-A2.

APPENDIX C

A table comparing the variation explained in the log-transformed kidney fat index (KFI) of Himalayan tahr by the seven candidate models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-114-A3.