Maternal Investment Strategies of Feral Goats at High Latitudes in Northwest Europe

Abstract

Reproduction is energetically expensive for mammals, and especially so during lactation. In large-brained mammals such a primates, females invest heavily in additional feeding to fuel the costs of lactation. The evidence is more ambiguous for ruminant ungulates. We examined the foraging costs of lactating female feral goats living under environmentally challenging conditions in the northwest of Scotland where these effects are most likely to be exaggerated. We show, using data from three separate study periods, that, compared to non-lactating females, lactating females do increase the time devoted to foraging, but only to a limited extent that is well below the theoretical requirements of their kids. We show that they are unable to reduce these costs by foraging on richer quality foods or reducing their thermoregulatory costs. As a result, they lose condition and are obliged to recoup these costs post-weaning. In doing so, they incur a double penalty: delayed return to reproductive condition and a high risk of mortality. At high latitudes, the costs that ungulate females face radically constrain the species' options.

Key Words: lactation, diet, thermal ecology, costs of reproduction

Highlights:

- Lactation is costly, obliging females to increase food intake or draw on body fat
- At high latitudes, goats increase foraging, but not enough to meet kids' demands
- Lactating females do not forage on richer foods, and can minimise thermal costs only to a limited extent
- As a result, females risk high mortality after weaning and are forced to reduce fertility

Introduction

While lactation brings substantial benefits to mammals by enhancing neonatal survival (e.g. Power & Schulkin 2013), the costs for the mother are significant. In contrast, the energetic costs of gestation are typically modest because the mammalian foetus is small relative to the mother (in primates, around 0.75% of the mother's BMR, or 0.58% of her total daily energy expenditure: Ulijaszek 2002). The costs of lactation arise in part because, after birth, the neonate increases rapidly in size (and is hence more energetically demanding) and in part because the process of lactation itself is energetically expensive. In mammals, around 20% of the additional energy (over and above the mother's own metabolic needs) required for lactation is devoted to the physiological processes of converting energy into milk (Blackburn & Calloway 1976; Robbins 1983). In addition, younger animals require higher protein or energy levels in their diet than adults (Arnold & Dudainski 1978). As the infant grows, this quickly becomes a considerable burden on the mother's foraging capacities. This inevitably has implications for how females manage their available time in order to optimise both their own and their offspring's survival.

As a general principle, species can opt to solve the energetic debt created by lactation in one of two ways: 'income breeders' seek to fuel the costs by increasing energy ingestion in proportion to demand (e.g. by devoting more time to feeding, increasing bite rate or being more selective in choice of foods) whereas 'capital breeders' build up fat stores ahead of time and draw on these to fuel lactation (or, alternatively, draw on existing body reserves to create an energy debt and then replenish this by feeding more post-weaning) (Drent & Daan 1980; Houston et al. 2007; Brogi et al. 2021).

In mammals, it has been suggested that lactating females are, generally speaking, ‘income breeders’ as they increase time devoted to feeding and/or select for nutritionally higher quality forage (Clutton-Brock et al. 1982a; MacWhirter 1991). Lactating red deer (*Cervus elaphus*), Stone’s sheep (*Ovis dalli stonei*), Colombian ground squirrels (*Spermophilus colombianus*), several South American monkeys (*Cebus* spp., *Alouatta* spp., *Cebus* spp.), guenons (*Chlorocebus* spp.), baboons (*Papio* spp.), gelada (*Theropithecus gelada*) and chimpanzees (*Pan* spp.) are all reported to spend more time foraging than non-lactating females and/or exhibit greater dietary selectivity than females that are not lactating (Altmann 1980; Clutton-Brock et al. 1982b; Seip & Brunnel 1985; Lee 1987; Dunbar & Dunbar 1988; MacWhirter 1991; McCabe et al. 2007; Murray et al. 2009; Dias et al. 2011; Dolotovskaya & Heymann 2020; Perwitasari-Farajallah et al. 2022).

In reality, most large-bodied mammals probably adopt a mixed strategy. Baboon (*Papio*) females increase feeding time through lactation (Altmann 1970) but also lose body condition (Bercovitch 1987; Kenyatta 1995). The resulting weight loss can be significant: Barrett et al. (2006) found that female baboons lost an average of 2.5 kg (about ~13% of body mass) over the first ~80 days postpartum. Significant weight loss during lactation has been widely documented in mammals (red deer *Cervus elephas*: Loudon & Kay 1984; cats *Felis catus*: Martin 1986; hamsters *Phodopus sungorus*: Weiner 1987; ringtailed lemurs *Lemur catta*: Pereira 1993; badgers *Meles meles*: Woodroffe & MacDonald 1995; humans *Homo sapiens*: Dewey et al. 1993).

The problem, however, is to know how large the energy deficit that a female incurs during lactation actually is: only then do we have a realistic idea of the magnitude of the problem she has to solve. Altmann’s (1980) maternal time budgets model provides a promising tool for this because it allows us to estimate, on a real time basis, the additional foraging time that a female needs if she is to fuel lactation only on an income basis. Her model assumes that, if primates are income breeders and pay all the costs of lactation by additional foraging, time spent feeding by lactating mothers should increase as a linear function of infant metabolic body mass (mass$^{0.75}$). The model has been tested on five different primate populations, with broadly positive results (allowing for differences in habitat quality) (Altmann 1980; Dunbar & Dunbar 1988; Kenyatta 1995; Lycett et al. 1998; Barrett et al. 2006).

Altmann's model thus provides us with a baseline against which to test the extent to which a species is an income breeder. Only if females cannot meet the energy demands of lactation by increasing energy throughput (the income stream) should they resort to other options. This might include foraging more efficiently (e.g. selecting nutritionally richer food sources or reducing thermal demand by foraging in less exposed micro-habitats) (alternative income stream possibilities) or metabolising fat reserves (the capital stream). Due to scaling effects, large-bodied animals are able to tolerate some weight loss if they are unable to meet their daily nutritional requirements in full (Schmidt-Nielsen 1984). This might allow them to adopt a more tactical approach in which they switch between the two strategies depending on environmental conditions (Kerby & Post 2013; Stephens et al. 2014; Williams et al. 2017). In benign conditions, a species might be able to cover all the costs of lactation by feeding more efficiently or at higher rates, but in challenging conditions, they may have to adopt a mixed strategy. Because a capital-based strategy in which the female relies on metabolising her own body mass to fund lactation necessarily puts both her life and that of her offspring at risk, an income-based strategy should always be the preferred option. The question of interest always is where and to what extent a female is prepared to incur these risks.

We explored this question in a feral goat (*Capra hircus*) population on the Isle of Rùm, NW Scotland. Rùm (~57ºN) lies close to the limit where this originally subtropical species can survive in the wild (~60º latitude: Whitehead 1972; Dunbar & Shi 2013). Because their tolerance of variations in thermal environment is very low, thermoregulation is a serious issue for mammals living at high latitudes (and high altitudes). The need to maintain constant body temperature becomes exponentially expensive in energetic terms as temperatures fall (Mount 1979), and considerable energy savings can be achieved by avoiding cooler environments (e.g. by spending more time lying to reduce convective heat loss, by making more use of sheltered locations or by staying at lower altitudes) or by foraging on energy-rich foods.

These problems are compounded for the goat population on Rùm because of the mountainous nature of their habitat. Unlike the red deer on Rùm , the goats occupy the more rugged westernmost coastal fringes of the island, where 200 m sea cliffs lead up to stoney hilltops above 400 m asl. In addition to the thermal effects of altitude (equivalent to 1ºC reduction in mean temperature per 100m), wind sheer effects mean that wind speeds become progressively faster with altitude, adding an additional cooling effect: at 200m asl, wind speeds are ~70% higher than at sea level, effectively reducing experienced temperatures by a further 2.5ºC. Combining these two effects means that remaining near the beach rather than accompanying other goats up the cliff face during the day’s foraging would reduce the experienced thermal environment by ~4.5ºC compared to the clifftops (at 200 m asl), and by ~9 ºC compared to the hilltops beyond (at 400m asl), yielding very significant energy savings (albeit at the cost of a more limited diet).

Ruminant ungulates face an additional problem not encountered by frugivorous primates: microbial digestion of cell walls in the forestomach assisted by the mechanical processing of fibre length during rumination (Dunbar & Bose 1991). The very narrow constriction of the reticulo-osmasal junction separating the front two chambers from the back two chambers of the ruminant stomach, mechanical breakdown of fibre size via rumination is necessary to clear the forestomach before feeding can resume. Rumination places additional demands on their time budget because the bacteria responsible for gut fermentation are extremely sensitive to body temperature, such that the processes of digestion automatically shut down if body temperature is elevated by any form of activity (van Soest 1994). Because of this, ruminants have to rest in order to allow fermentation to take place. This may be especially challenging for populations living at high latitudes where resource availability is both seasonally and annually unpredictable and of generally poor nutritional quality (hence requiring considerable fermentation). If a female cannot meet the extra energy demand for lactation by increasing feeding time or eating more digestible plants, then she may be forced to draw on her body reserves by becoming a capital breeder at the potential cost of placing her own survival at risk.

We frame our analysis around Altmann's maternal time budgets model since it provides clear quantitative predictions of what lactating females should do if they are pure income breeders. Our strategy is as follows. First, we ask whether the females behave as income breeders by increasing feeding time in proportion to their kid's demand for milk, as predicted by the Altmann model (adjusted for the larger birth weight and faster growth of goat kids). In effect, we ask: do the females compensate for the costs of lactation in real time by increasing their feeding to match infant demand? If they do not do so fully, we can then ask how they make up the deficit. We consider two broad possibilities that differ in their time scale: by reducing their own energy demand in the short term (on the scale of days or weeks, either by foraging more efficiently or reducing their thermoregulatory costs) or by a longer term strategy (on the scale of months) of drawing on fat reserves in the short term and then replenishing these at some future time.

We begin by testing whether females adhere to an income-based strategy by asking, first, whether lactating females devote more time to feeding than females who did not reproduce that year (‘dry’ females) (RQ1a). We use the time budgets of dry females as a baseline because we need to control for changes over time in both daylength and forage quality. At the latitude of Rùm, daylength (Dunbar & Shi 2013) and forage quality (Shi 2002) improve dramatically during the spring and early summer, and this might reduce the need to spend so much time foraging. We then ask whether lactating females match the quantitative predictions of the Altmann model, since this defines the magnitude of the energetic cost the females incur (RQ1b). The extent to which they fail to match the model predictions defines the energy debt they need to recoup.

If females face an energy debt that they cannot replenish on a daily basis, they must draw on fat reserves to fill the gap. They can recoup this debt in one of two ways. On a shorter timescale they may be able to reduce overall foraging time demand either by feeding on richer foods or by minimising thermally stressful exposure. On a longer time scale, they may absorb the cost through metabolising fat reserves in the short term and recoup this later post-weaning. Our second question addresses the first possibility by asking whether females reduce their own energetic costs during the period of lactation. We consider a number of possibilities: by feeding in nutritionally richer habitats (RQ2a), by spending more time ruminating in order to extract more nutrients from their ingesta (RQ2b), or by reducing exposure to wind chill so as to conserve energy either by spending more time lying (RQ2c) or by making more use of shelter (RQ2d) or by ranging at lower altitudes (RQ2e).

Finally, we ask whether the costs of lactation force females to go into energy deficit on a longer timescale. In the absence of actual weight data (we were not allowed to capture the animals), we determined this indirectly in two ways: by determining whether there was a decline in female body condition across the period of lactation (RQ3a) and whether this was reflected in higher female mortality during the subsequent autumn and winter when the goats are all under considerable nutritional stress (RQ3b). We base this on the fact that red deer females on Rùm experience significant weight loss and elevated mortality risk in those years when they rear calves to weaning (Clutton-Brock et al. 1987), suggesting that this environment may be very taxing for lactating females. We then ask whether pregnant females anticipate an energy debt from lactation either by feeding more during their autumn pregnancy so as to build up fat stores (RQ3c) or by continuing to feed at higher rates for longer after weaning in order to recoup their energy debt (RQ3d).

Methods

Study area and animals

The study was carried out at Harris, on the west coast of the Isle of Rùm, NW Scotland (57°0′N, 6°20′W). The goat population has been feral here since the 1770s. Female heft groups of various sizes occupied semi-exclusive territories along a 10-km stretch of coastal cliffs (Gordon et al. 1990; Dunbar 2025). Although the population was subject to intermittent culling in the 1950s and 1960s, no culling had taken place for ~20 years prior to the start of the present series of studies in the 1990s. The Rùm goats have a main birth season between mid-January and early February, with kids weaned and independent at 8-10 weeks of age (Fig. 1). Because many kids die within the first few weeks after birth, there is a secondary rut in the following spring with a second birth peak in July-August (accounting for 22% of all births) (Dunbar 2025).

The main study site for the present studies consisted of a large, flat raised beach (Harris Bay) dominated by semi-natural *Agrostis-Festuca* grassland, with a narrow rocky foreshore; to the north and south, the foreshore gave rise to extremely steep ~200m sea cliffs dominated by grasses and heather (*Erica*), interspersed with rock cliffs and scree slopes. The flatter upper parts of the sea cliffs had a mixture of vegetation types (*Calluna* heath, wet heath, blanket bog, *Nardus* heath, *Schoenus* fen, *Molinia* flush, herb-rich heath and marsh), rising to bare, stoney hilltops above 400 m. Rùm has an Atlantic climate, with high rainfall, frequent winter gales, and low but highly variable temperatures with mean monthly temperatures varying across the year between 4-14°C (Dunbar 2025). The landscape is often snow-covered in winter, especially at higher altitudes on the hilltops (>400 m asl). Mean and minimum monthly temperatures for the study site are from Dunbar (2025); average monthly daylength is from Dunbar & Shi (2013).

In 2000, as part of a separate foraging ecology project (Shi 2002), vegetation biomass production and energy and protein content were measured in 120 exclusion plots (each of 100 cm^2) distributed among nine principal vegetation habitats. Plots were clear-cut to measure biomass production at the end of each month. Nutrient content was determined by the UK Government Agricultural Advisory Service (ADAS) laboratory, Wolverhampton. Once growth had ceased, new plots were added for nutrient content of the standing crop. Fig. 2 plots mean protein content and digestibility (the two main factors determining accessible energy content) of forage across the year. Forage quality increases progressively through the spring (the main period for lactation), peaking in early summer (the main period for post-weaning recovery), before declining again through the autumn and winter.

At least at this latitude, goats are only active during daylight; at night, they typically sleep in groups on the beach or in the many caves at beach level. During the day, the goats forage out onto the grasslands (in Harris Bay) or up onto the cliff tops, always returning to beach level at night. Mean minimum ambient temperatures at beach level were ~4.0°C warmer than those at an altitude of 400m asl on the adjacent hilltops, with temperatures inside the beach level caves used as night time shelters being a further 2.0°C warmer (Dunbar & Shi 2013; Dunbar 2025). Long term mean monthly temperature data were sourced from the UK Meteorological Office for Tiree (the nearest weather station, 60 km southwest of the study site) (https://www.metoffice.gov.uk/pub/data/weather/uk/climate/stationdata/tireedata.txt).

The results reported here are based on studies carried out during the 1993, 2004 and 2006 winter birth seasons. The 1993 study focussed only on the period of lactation up to weaning. To explore the possibility that females might recoup an energy debt incurred from lactation by continuing to feed at high rates after weaning, the 2004 and 2006 studies extended sampling through the summer to cover the post-weaning period. In addition, the 2006 study commenced sampling during the autumn when females were pregnant in order to determine whether they attempted to build up an energy surplus before giving birth. To calculate mortality rates, we use demographic and lifehistory data for known individuals from studies in 1981/1982 and 2005/2006.

Data sampling

All data were collected during 30-min focal follows of individually identified females, conducted between 08:00 and 18:00 h. Sample sizes were: six lactating and three dry females for the 1993 cohort (mean of 57 focal follows, or 28.5 h, per female); eight lactating and four dry females, plus four females whose kids died soon after birth, for the 2004 cohort (mean 85 focal follows, or 42.5h, per female); and three lactating and six dry females (three of whom had given birth the previous year) in the 2006 cohort (mean 124 focal follows, or 62 h, per female). The 1993 study was conducted on the GnP and Ruincival heft groups whose ranges lay immediately north and south, respectively, of Harris Bay; the 2004 and 2006 studies were carried out on the Harris heft group that had colonised Harris Bay in the later 1990s (see Dunbar 2025).

In the focal samples, female behaviour (classified as feeding, moving, standing or lying; whether or not ruminating and, if feeding, the habitat type), kid behaviour (including suckling, distance of mother to kid and mother-kid interactions) were scan-sampled at 60-sec intervals. In addition, the altitude, vegetation type and whether or not the female was in shelter from the prevailing wind were recorded on each scan. Vegetation types were categorised into ~9 major types based on the standard Ferreira (1970) Rùm vegetation map (see online Supplementary Methods, Table S1). Weather conditions (including wind speed on the Beaufort scale), the number and identity of other group members present and (in the 2006 study) the female's body condition were recorded at the start of each focal sample. Body condition was recorded visually on a 5-point Likert-type scale based on that used by British shepherds for sheep; it indexes the degree to which hip bones are covered by flesh and reflects body fat stores. We adapted this scale for visual assessment (0 = hips well padded by muscle, bones not visible; 5 = no flesh cover, hip bones clearly projecting).

The data are provided in the four online Supplementary Information files [Rum 1993 dataset; Rum 2004 dataset; Rum 2004 habitat use; Rum 2006 dataset].

Statistical analyses

We test the RQ1 in two ways. First, we ask whether lactating females spend more time feeding than dry females (RQ1a) and, second, we test whether the regression slope for time spent feeding by lactating females increases linearly with kid age in the way predicted by the Altmann model (RQ 1b). For the first test, we compared time spent feeding each calendar month by lactating and dry females during the spring lactation period (January to April, inclusive). We use calendar month rather that kid age so as to be able to compare lactating and dry females on the same time base. Since all winter kids are born within the same 3-week time window from mid-January on Rùm, calendar month is approximately equivalent to kid age.

Since daylength at the latitude of Rùm varies between 7.7 hr in December and 17.2 hrs in June, mean monthly feeding time was adjusted for daylength (based on Dunbar & Shi 2013) so as to give the equivalent of a standard 12-hr day (as used in the Altmann model). We used a GLMM model with mean percent time feeding in each month, with month nested within individual nested within reproductive status (lactating or dry) nested within study year, with a gamma probability structure since the outcome variable is highly skewed. To test whether lactating females matched the predictions of the Altmann model (RQ1b), we regressed adjusted time spent feeding on calendar month, and compared the slopes between lactating and dry females and against the slope predicted by the Altmann model.

Altmann (1980) parameterised her model for baboons (a cercopithecine primate). Goats differ from primates in being absolutely and relatively much larger at birth and growing much faster: goat kids are weaned at around 6-8 weeks of age (Fig. 1) and become reproductively active at the end of their first year, whereas cercopithecine monkeys are weaned at around 8 months and do not undergo puberty until they are 4-5 years old. To parameterise the model for goats, we used a mean adult body mass of 46.7kg, kid a mass at birth of 2.7kg, and a kid growth rate of 0.182 kg/day based on domestic goats in poor quality outdoor environments in New Zealand (Bajhau & Kennedy 1990). The Altmann model was benchmarked to the observed feeding time at the end of pregnancy; for present purposes, we used the time spent feeding by the sample of non-lactating females in January.

Analyses for diet are based on the 1993 and 2004 studies (RQ2a); the proportions of time spent ruminating (RQ2b) and lying are based on the 2004 and 2006 studies (RQ2c), while those for the proportion of time spent in shelter (RQ2d) and at different altitudes (RQ2e) are based on the 1993 study. Data for rumination and lying were adjusted for daylength, as above. Comparisons between lactating and dry females used either GLMM (structured as above) or, when only data from one study are being analysed, matched-pairs t-tests, standard ANOVA or multivariate regressions (with calendar month, mean temperature and mean wind speed as predictor variables).

Finally, since we were not permitted to capture and weigh the goats (and hence could not measure weight loss directly), we tested whether lactating females draw on body fat reserves to fuel lactation indirectly by examining variation across time in body condition (RQ3a) (from the 2006 study) and the mortality risk that females run (RQ3b). To determine the mortality risk that lactating versus dry females run, we combine individual lifehistories for 93 female-years from the 1981-2 study and 57 female-years from the 2005-2006 studies. We then ask whether lactating females fed for longer during pregnancy than dry females (RQ3c) (from the 2006 study) or continued to feed for longer post-weaning (RQ3d) (from the 2004 and 2006 studies).

In most of these cases, we test an *a priori* directional hypothesis (lactating females do something more, or less, than dry females); formally, all such tests are 1-tailed in the appropriate direction. In other words, when testing for a predicted positive difference, any observed difference in a negative direction has a significance $p_{1(+)} = 1-(p_2/2)$, where $p_{1(+)}$ is the likelihood that the observed negative difference actually reflects a positive difference in the predicted direction and p_2 is the conventional 2-tailed p-value associated with the observed value of the statistic. The reverse obviously holds for a negative prediction. All such cases are indicated as being 1-tailed; all other cases are 2-tailed with direction unspecified.

Ethical Note. Since the studies were purely observational, there was no requirement for ethics review.

Results

We first determine whether lactating females spent more time feeding than non-lactating females during the period when kids were being suckled (late January through April) (RQ1a). We then test the Altmann model prediction that feeding time should increase over time as the kid's energy demand increases (RQ1b). In the following subsections, we test whether lactating females either compensate dietetically for the energy costs of lactation or reduce their thermal costs (RQ2) and then whether the goats opted to draw on fat reserves to fuel lactation thereby incurring an elevated mortality risk and/or fed longer during late pregnancy or post-weaning (RQ3).

Research Question RQ1: Do lactating females feed more than dry females?

Fig. 3 tests RQ1a by plotting the mean time spent feeding by lactating and dry females in each of the three study years. Table 1 gives the GLMM analyses of these data, controlling for study, month and individual female: during the period of peak lactation (January through April), lactating females spent significantly more time feeding than dry females. The estimated marginal means (controlling for study and month) suggest that the difference was ~7 percentage points (Fig 4).

Although lactating females fed more than dry females, this does not necessarily mean that they match the predictions of the Altmann model (RQ1b). Fig. 5 tests this by plotting the mean number of hours a day spent feeding (adjusted for daylength to a constant 12-hr daylength) by lactating and dry females, as well as by females whose kids had died soon after birth, for the 2004 sample. The upper heavy line plots the prediction from the Altmann (1980) model (parameterised for goat adult and neonate body masses and kid growth rates in poor quality temperate environments), while the uppermost dotted line plots average daylength. The fine uppermost line plots the total feeding plus rumination time (estimated from the 2006 dataset at an additional 7.6% of feeding time) added to the predicted feeding time. Since the parameter *A* that converts energy intake into feeding time is not known for goats (or baboons), we follow Altmann and set the base feeding time at birth to the time that dry females spent feeding in February. Although feeding time clearly increases across months as the kids age, the slope is much shallower than that predicted by the Altmann model (and lower than the average slope for baboon mothers). After the first month or so, the time lactating mothers devote to feeding does not come close to matching their kid's energetic demand. More importantly, feeding and ruminating time exceed available daylength from around mid-March (allowing for an overall average of 3.0% of time spent moving from the 2006 dataset).

The slopes for time devoted to feeding across months (treated as ordinal numerical values) for the two reproductive conditions clearly do not differ from each other. More importantly, both are significantly shallower than the slope for the model prediction (Fig. 6; one sample t-tests against an expected model slope of 36.66: lactating females, $t_{11}=-11.90$, $p<0.0001$;

dry females, $t_9=-4.80$, $p=0.001$, 2-tailed in each case). Lactating females are clearly not managing a wholly income-based lactation strategy. An important point to note is that if lactating females were to adhere to the Altmann model, they would run out of daylight time for feeding by mid-March, well before weaning, in large measure due to the impact of rumination time.

Taken together, these results suggest that females do spend more time feeding when they are lactating, but do not do so sufficiently to meet the energetic demands of their kid: lactation causes them to incur a significant energy debt. Since females are not behaving as pure income-breeders with respect to the costs of lactation, we need to ask whether, during the lactation period, they are adjusting their behaviour in a way that would offset some of the costs of lactation. We consider this possibility in the following section.

Research Question RQ2: Do lactating females use their time more efficiently?

We test five possible ways that lactating females might reduce the energy (and hence time) costs of lactation: compared to dry females, they might make greater use of more nutrient-rich food sources (RQ2a), devote more time to rumination in order to extract more nutrients from their ingesta (RQ2b), spend more time lying as opposed to standing (in order to reduce body surface exposure to convective heat loss) (RQ2c), or spend more time in sheltered positions (RQ2d) and/or at lower altitudes (RQ2e) (in order to reduce the effects of windchill). The first two address the income side of the energy equation, the latter three the expenditure side.

The relative frequencies with which females fed in the different habitat types are shown in Fig. 7. With the exception of seaweed on the beach (paired-samples t-tests with females matched for age: t_8=-3.59, p=0.007) and *Schoenus* fen (waterlogged sedge-dominated marsh) (t_8=2.54, p=0.035) (lactating non-lactating females females avoided the first, whereas non-lactating females seemingly avoided the second: paired-samples t-tests, 1993: $t_8 \leq 2.06$, $p \geq 0.073$; 2004: $t_6 \leq 2.15$, $p \geq 0.075$), there are no significant differences in the time spent foraging in each habitat type by the lactating females compared to dry females. Although there are some differences between the two study years (e.g. greater use of herb-rich heath and grassland in 2004 than in 1993), this may have more to do with the fact that different (albeit adjacent) heft groups were sampled than with any meaningful year-to-year differences in forage availability.

Fig. 8 tests whether lactating females spent more time ruminating in order to extract more nutrients from their ingesta (RQ2b). In fact, lactating females spent slightly less time ruminating than other females, though the difference is not statistically significant (GLMM analysis: Table 2). Fig. 3(b,d,f) and Table 2 test whether lactating females spent more time lying to avoid exposure to wind (RQ2c). The GLMM model for percent time lying, adjusted for daylength, indicates that the difference between lactating and dry females is marginal (means of 16.6% vs 18.2%) and not significant, controlling for study, month and individual identity.

Similarly, lactating females do not spend more time in shelter than dry females (Fig. S1a; means: 20.1±20.3% vs 15.4±15.9%, respectively; t_{54}=-0.97, p=0.367) or at lower altitudes (Fig. S1b; mean altitude: 238.3±134.6 vs 183.1±158.9 m asl, respectively; t_{54}=-2.05, p=0.045) (RQ2d and RQ2e). Nonetheless, there were some significant differences between lactating and dry females in the way they responded to the thermal environment (Table 3). Dry, but not lactating females, significantly reduced their use of shelter when temperatures were warmer (Fig. 9a: p=0.047 vs p=0.334 and p=0.082 vs p=0.934 for the two studies, respectively, controlling for month and windspeed), suggesting that lactating females might have been trying to avoid being unnecessarily exposed when conditions were especially adverse. Similarly, lactating females, but not dry females, did spend significantly more time at lower altitudes on windier days (Fig. 9b: p=0.043 vs p=0.545, controlling for month and ambient temperature). However, contrary to expectation, lactating females in the 2004 cohort spent significantly less time in shelter on windier days, despite the fact that it was windier in 2004 than in 1993 (mean Beaufort = 3.71, range 1-6, vs 2.65, range 1-7, respectively).

In sum, there was little evidence that lactating females made consistent use of any behavioural ways to increase their energy intake (RQ2a,b) or reduce their thermal exposure (RQ2c-e), except in extreme weather conditions. The latter clearly offers some support for RQ2, but the effect does not appear to be large enough to eliminate the lactation debt. This implies that they must rely on fat stores to some extent. In the next subsection, we consider evidence for this.

Research Question RQ3: Do lactating females use fat reserves to fuel lactation?

We test Research Question RQ3 in two ways: first, by determining whether there is any evidence that lactating females went into energy deficit (either in terms of body condition or higher mortality risk) (RQ3a and RQ3b) and, second, by determining whether pregnant females fed more during the autumn so as to lay down fat stores in anticipation of the costs of lactation (RQ3c) or continued feeding longer into the summer months after kids are weaned in order to recoup lost fat stores (RQ3d).

Fig. 10 plots the mean (±1 sem) monthly body condition scores for lactating and dry females across months (RQ3a). Overall, there is a steady decline in condition across the autumn months through winter into the summer. Although lactating females typically seem to have higher condition scores than dry ones, the differences are not significant either across the whole sample or separately within the pregnancy, lactation and post-weaning periods (Table 3). However, the fact that, with the exception of December, lactating females are in better condition than dry females in every month might be explained by the fact that females who come into oestrus and conceive are those that are in better condition during the August rut (which in turn might be related to whether they had a kid the previous year).

Fig. 11 explores this in more detail by examining mean monthly condition score as a function of whether or not the female produced a live kid in consecutive years in the 2005-2006 birth seasons. Overall, average condition scores differed significantly between the four reproductive groups (GLMM, with category>individual>month structure: $F_{3,208}=3.87$, $p=0.01$; Scheffé tests yield a significant pairwise comparison only between the 1-0 and 0-1 groups: $p=0.007$). What is readily apparent is that females who kidded in 2005 but not 2006 had much lower condition scores in 2006 than those who kidded in 2006 but not 2005. Those that failed to kid in either year had autumn scores similar to those who kidded in 2006, but lost condition during the winter: they may well have conceived during the August 2005 rut, but lost the kid late in pregnancy or soon after birth. The only female (of 26) who reproduced in both years was clearly in much better condition across both years than the average.

As a test of RQ3b, Fig. 12 plots the distribution of male and female deaths across the year from the detailed demographic records in the 1980-1 study. The two distributions are not positively correlated ($r=-0.017$, $N=12$, $p=0.522$ 1-tailed), suggesting that they do not reflect the same underlying cause (such as weather or changing forage quality). Female deaths exhibit a bimodal distribution with peaks in April and August, in both cases following the two lactation peaks. In contrast, 65% of male deaths occurred in autumn months (September-December), mainly as a result of the exertions incurred during the August rut (Gordon et al. 1987; Dunbar et al. 1990; Dunbar 2025). For both sexes, autopsies indicated that the principal cause of death was starvation (very poor body condition) (Dunbar 2025).

Fig. 13 plots the ratio of the probability that a female aged *x* will die to the probability that she will have given birth earlier that year. There is a significant cubic regression ($r^2=0.933$, $F_{3,7}=32.68$, $p=0.0002$), indicating a bimodal distribution: younger (1-2 year old) and older (9-11 year old) females have a significantly higher mortality risk if they kid compared to females in their reproductive prime (aged 4-8 years, who also have the highest fecundity rates: see Dunbar 2025 [Fig. 9]).

Taken together, these results offer support for RQ3a and RQ3b: females do draw on their fat reserves during the course of lactation, and this puts them at significant mortality risk later in the year. Even if the female survives, it takes her a full year to recoup these costs so as to be in good enough condition to conceive again, hence explaining the fact that females typically only give birth in alternate years.

To determine whether pregnant females anticipate the costs of lactation by feeding more during pregnancy (RQ3c) and/or feed more later post-weaning in order to recoup their energy debt (RQ3d), we ran GLMM analyses of time spent feeding by females during the autumn and early winter months (September-December, when females are pregnant) and during the post-weaning early summer months (May-June). Table 1 indicates that, although there is a modest post-weaning catch-up by lactating females, in neither period did lactating females feed significantly more than dry females. Note that, due to both the short daylength during winter and poor nutritional quality of the forage, realistically the opportunities to exploit higher feeding rates during pregnancy as a mechanism for laying down fat stores in anticipation of lactation in the spring are in fact probably very limited.

Discussion

We have shown that, in the extreme environment of northwest Scotland, the costs of lactation impose considerable demands on female feral goats that they can only partially meet by devoting more time to feeding (income-based reproduction). Although they make some effort to reduce the energetic costs they face, they seem to have only a very limited capacity to forage in ways that either increase access to nutrients or reduce the costs of thermoregulation. Instead, it seems that they switch to a capital-based strategy by drawing on fat reserves. This seems to have two consequences for them: one is that it increases the risk of dying as a result of overreach, the other is that those that survive lactation take such a long time to recover that they are only able to reproduce in alternate years.

The magnitude of this cost is evident in the fitness consequences. Mean age at death for the Rùm females is ~7 years of age for those that survive to reproductive age (12 months)

(Dunbar 2025). For a seasonal breeder, the maximum possible average lifetime reproductive output is just 6 kids. Since most females on Rùm only reproduce every other year, this reduces to three kids, half of whom will die before puberty (Dunbar 2025), leaving a net lifetime reproductive output of just 1.5 surviving offspring (i.e. just below replacement rate). In other words, although the goats try to act like income breeders, they cannot match the lactation demand imposed by a large, fast-growing kid, even though these are weaned after just a few months. As a result, they are forced to become capital breeders and trade off whatever fat stores they have.

On Rùm, the bulk of the plant biomass growth occurs during the spring and early summer, such that by late summer the amount of nutrient-rich new growth is close to zero (Fig. 2). Females that kid in the winter who then try to replenish their fat stores during the summer face an uphill battle against declining resource availability and shortening days. Females that kid in the summer face especially challenging conditions because they give birth just as plant growth comes to an end. This might account for the surprisingly high peak in female mortality in August, as well as its greater proximity to the onset of summer births (Fig. 10). At least in the case of the Rùm goats, direct within-species competition can be excluded as a likely explanation for between-year variation in either feeding time or female mortality: Shi & Dunbar (2005) found little evidence for direct competition, and even when animals did displace each other while foraging it had very little effect on their foraging efficiency.

In this respect, the goats mirror the sympatric red deer, who, despite being native to this environment and considerably larger-bodied, have the same biennial cycle of reproduction and exhibit a similar pattern of a significantly increased mortality risk in the year when a female reproduces (Clutton-Brock et al. 1987). This suggests that most ungulates probably experience high latitude habitats as challenging. The difference between the native deer and the invasive goats is that the goats' reproductive rates are so low that they are often at or just below the demographic replacement rate whereas the deer seem to be able to cope better. This is reflected in a contrast between the goat population's long term trajectory (which remained broadly stable from the 1960s until the 2010s: Dunbar 2025) whereas the deer numbers have increased consistently year on year (Clutton-Brock et al. 2002).

That lactation at these latitudes is stressful for female goats is evident from the fact that, in New Zealand, free-ranging females lost as much as ~10 kg (20% of their body mass) by the end of lactation (Bajhau & Kennedy 1990). For most large-bodied mammals, this level of fat loss is sufficient to shut down the menstrual endocrinology system in order not to overburden the female (Dunbar & Shultz 2021). Different caprine species, however, may solve the problem of weight loss in different ways. Bighorn sheep (*Ovis canadensis*) contrast with the Rùm goats in that they do not spend significantly more time foraging during the summer period when their lambs are suckling than non-lactating females do (Ruckstuhl & Festa-Bianchet 1998), but do increase time spent foraging as well as bite rate during the autumn following weaning. Ruckstuhl et al. (2004) suggested that the ewes compensate for the body mass lost during lactation by not reducing their feeding rates during the autumn in the way that non-lactating ewes do. Their much larger body size may allow them to exploit the benefits of scaling to tolerate greater loss in body weight (Schmidt-Nielsen 1984). In contrast, lactating female alpine ibex (*Capra ibex)* spend significantly more time grazing than non-lactating females, and feed more quickly (higher bite rates) (Neuhaus & Ruckstuhl 2002). Lactating and non-lactating females of the Cantabrian chamois (*Rupicapra pyrenaica*), however, do not seem to differ in feeding time, suggesting that lactating females do not, or cannot, increase forage intake (Pérez-Barberia & Nores 1996).

Some of these differences may reflect habitat rather than species differences, and within-species studies based on a wider range of habitats are needed to clarify this. Nonetheless, caprines as a group clearly contrast strikingly with seals: as the ultimate mammal capital-breeder, seals store up fat reserves during the non-breeding season to meet the very high energy demands of lactation, probably because being away foraging while lactating would put the pup at significant mortality risk on the crowded breeding beaches (Fedak & Anderson 1982).

One of the constraints that ungulates face is that forage intake, and therefore foraging time, is a direct function of the speed at which plant tissue can be digested (Spalinger et al 1988), with digestive capacity limited by stomach size and rumen turnover rates (Robbins 1983; van Soest 1994). Incisor bar size (Gordon & Illius 1988; Gordon et al. 1996) and plant structure (Illius & Gordon 1993) can add a further constraint. These effects may prevent goats from compensating fully by increasing the rate of plant matter consumption during the lactation period. Lactating deer hinds (which are much larger in body size) adjust their diet to feed more on grasses and less on heather compared to yeld (i.e. dry) hinds (Blaxter *et al* 1974). Although forage choice by the goats certainly changed over the course of lactation, much of this can probably be attributed to differences in food availability (and the constraint imposed by the kid’s mobility) rather than preference, combined with the fact that goats are browsers rather than grazers. An additional problem for the Rùm goats is that they are restricted in their ability to seek out high quality food sources by their kids’ limited mobility in a physically and thermally challenging landscape. Kids are born at beach level where it is warmer, and are unable to climb the very steep sea cliffs until they are at least a few weeks old, so that the mother is forced to remain near the beach. Even once the kid can cope with the climbs, they are slower and less nimble than adults and older immatures, so that the mother’s capacity to move between food patches is greatly reduced. Females with kids at heel were often left foraging on their own for this reason (Calhim et al. 2006).

The goats' failure to match the Altmann (1980) income model has important implications in relation to offspring growth rates and the capacity to produce large-brained offspring. In comparison with primates, goat kids are heavier at birth than primate infants, grow much faster and mature considerably earlier. The typical large-bodied baboon, for example, weighs in at only 0.775 kg at birth (for a mother that weighs 9-11 kg) and its rate of growth through to weaning averages around 0.005 kg a day (Altmann 1980); goat kids average 2.7 kg at birth (for a mother that weighs ~20 kg), and grow at a rate of 0.182 kg/day (Bajhau & Kennedy 1990). In other words, goat kids grow ~35 times faster than baboons, in addition to their larger size at birth. On Rùm, most goat females reproduced in their second winter. In contrast, smaller bodied baboons don't give birth for the first time until they are 4-5 years of age, allowing females to build up better body condition before starting reproduction. In addition, primates spread the cost of investment in lactation over a much longer period than goats do. This has significant implications for ungulates' capacity to grow large-brained offspring: without a major change of dietary strategy and a much slower lifehistory, it would be impossible for them to do so.

In sum, goats at high latitudes face significant challenges in respect of the costs of lactation. These results highlight the enormous costs that tropical mammals with precocious offspring face when attempting to invade high latitude habitats. Ultimately, the principal constraint is not so much the animals' own survival as their ability to provide sufficient energy for their dependent offspring, and the drain that attempting to do so imposes on their own capacity to survive. This may in part explain the relatively low species diversity of large mammals at high latitudes other than of those species that keep their offspring in underground nests.

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Statement of Ethics

The research reported herein was purely observational and did not require ethical approval.

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Conflict of interest

The authors declare no conflicts of interest.

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Legends to Figures

Fig. 1. Frequency of suckling per hour by kids of different age (surviving kids only), indexed as the proportion of 60-sec scans on which the kid was on the teat in focal follows of the mother. Data for the 2004 birth cohort (see Methods).

Fig. 2. Vegetation availability across the main lactation and post-weaning period, determined in 2000 from 120 exclusion plots, each of 100 cm^2, distributed across the nine vegetation communities in the goat study area. Source: Shi (2002).

Fig. 3. Time spent feeding and resting (lying) as a function of age of kids for the (a, b) 1993, (c,d) 2004 and (e,f) 2006 birth cohorts. Filled symbols (solid line): lactating females; grey symbols (dotted line): females who lost their kids after birth; unfilled symbols (dashed line): dry females.

Fig. 4. Estimated marginal means (±1 sem) for percent of time spent feeding for lactating and dry females for the data in Fig. 3, as a function of study year, controlling for monthly variation in daylength.

Fig. 5. Mean number of hours per day spent feeding by lactating females (solid symbols, long dashed line), females whose kids had died shortly after birth (grey symbols, short dashed line), and dry females (unfilled symbols, dot/dashed line) over time, from the 2004 study, corrected for daylength to a constant 12-hour day. Also shown is daylength across the

months (upper thin dotted line), the feeding time for lactating females predicted by the Altmann (1980) maternal time budgets model (heavy black line) and the additional time required for rumination (thin solid line).

Fig. 6. Mean (±1sem) slope for time devoted to feeding (adjusted for daylength to a constant 12 hrs) regressed on ordinal calendar month (January = 1) for lactating and dry females in each of the three studies. The horizontal dashed line is the equivalent slope for the Altmann model.

Fig. 7. Percentage of feeding time devoted to different food types by lactating (filled symbols, solid line) and dry females (unfilled symbols, dashed lines) in successive weeks of the kid's life in the 1993 study (a, b, d, f) and the 2004 study (c, e, g). Seaweed was not recorded in the 1993 study.

Fig. 8. Percent of time spent ruminating ('chewing the cud') in each month by lactating females (filled symbols, solid line), dry females (unfilled symbols, dashed line) and females whose kids had died within a few weeks of birth (grey symbols, dotted line) for (a) the 2004 and (b) the 2006 study populations.

Fig. 9. Mean time spent (a) in shelter and (b) at different altitudes by lactating (filled symbols, solid line) and dry females (unfilled symbols, dashed line) in each week of the kid's life, plotted against mean temperature that week at the study site, for the 1993 study population.

Fig. 10. Mean±1 sem condition score for 6 lactating (filled symbols) and 24 dry (unfilled symbols) females in the 2006 study. Scores are monthly averages for each female.

Fig. 11. Mean condition score in each month for females who failed to reproduce in both 2005 and 2006 (0-0: dotted line; N=15), reproduced in 2005 but not 2006 (0-1: dashed line; N=5), reproduced in 2006 but not 2005 (1-0: fine solid line; N=5) or reproduced in both years (heavy solid line; N=1).

Fig. 12. Probability of adult female (unfilled bars) and male (filled bars) dying in different months of the year, overlain by proportional distribution of births (dashed line) Data from 1981-2 study. Source: Dunbar (2025).

Fig. 13. Female's relative mortality risk if she has a kid (indexed as the ratio of probability of dying at age x to the probability of having had a kid at age x) as a function of her age, based on 1981-82 demographic data.

Table 1. GLMM for percent of time spent ruminating and lying (corrected for day length to a 12-hr day), comparing lactating versus dry females.

Variable	F	df	p
%Feed: Lactation period (January-April: all three studies)			
Full model*	34.97	6,75	<0.001
Study	15.93	2,75	<0.001
Month	57.75	3,75	<0.001
Lactating vs dry	4.91	1,75	0.015†
Estimated marginal means: lactating = 74.9%; dry = 67.1%			
%Feed: Pregnancy (October-December: 2006 study only)			
Full model*	57.64	3,19	<0.001
Month	84.25	2,19	<0.001
Lactating vs dry	0.02	1,19	0.945†
Estimated marginal means: lactating = 82.4%; dry = 82.95%			
%Feed: Post-lactation (May-July: 2004 and 2006 studies)			
Full model*	3.32	2,6	0.107
Study	5.05	1,6	0.066
Lactating vs dry	0.07	1,6	0.898†
Estimated marginal means: lactating = 113.6%; dry = 117.4%			

* nesting structure: study > reproductive status > individual > month, with gamma distribution

† 1-tailed test of a specified a priori directional hypothesis (lactating > dry)

Table 2. GLMM for percent of time spent lying and ruminating (corrected for day length to a 12-hr day), comparing lactating versus dry females (2006 study only)

Variable	F	df	p
% Ruminate: Lactation period (January-May)			
Full model*	3.52	4,22	0.011
Month	4.01	6,22	0.007
Lactating vs dry	0.05	1,22	0.917†
Estimated marginal means: lactating = 13.2%; dry = 14.1%			
% Lie: Lactation period (January-May)			
Full model*	3.37	5,11	0.043
Month	4.15	3,11	0.027
Lactating vs dry	0.03	1,11	0.932†
Estimated marginal means: lactating = 16.6%; dry = 18.2%			

* nesting structure: study > reproductive status > individual > month, with gamma distribution

† 1-tailed test of a specified a priori directional hypothesis (lactating > dry)

Table 3. Multiple regression statistics for proportion of time spent in shelter and at different altitudes while foraging.

Status		predictor	slope	t	df	p
Dependent = shelter (% time) (1993)						
Lactating	full model			$F_{3,31} = 1.53$		0.227
		week*	-0.432	-0.17	31	0.867
		temperature†	-2.793	-0.98	31	0.334
		wind‡	-0.795	-0.27	31	0.791
Dry	full model			$F_{3,17} = 1.58$		0.232
		week*	5.146	1.77	17	0.094
		temperature†	-5.107	-2.14	17	0.047
		wind‡	2.681	1.01	17	0.329
Dependent = shelter (% time) (2004)						
Lactating	full model			$F_{3,28} = 7.58$		0.0007
		month*	-27.739	-0.68	28	0.504
		temperature†	2.242	0.08	28	0.934
		wind‡	-19.095	-2.24	28	0.034
Dry	full model			$F_{3,8} = 5.52$		0.024
		month*	103.054	1.54	8	0.162
		temperature†	-97.400	-1.99	8	0.082
		wind‡	1.450	0.09	8	0.928
Dependent = ln(mean altitude, m asl) (1993)						
Lactating	full model			$F_{19,36} = 6.02$		0.002
		week*	0.127	1.66	31	0.108
		temperature†	-0.002	-0.03	31	0.978
		wind‡	-0.187	-2.11	31	0.043
Dry	full model			$F_{3,17} = 0.79$		0.514
		week*	-0.267	-1.39	17	0.182
		temperature†	-0.002	-0.03	17	0.144
		wind‡	-0.187.	-2.11	17	0.545

* week or month from start of birth season (mid-January)
† mean ºC
‡ mean Beaufort wind speed scale [analogue scale 0-13]

Table 4. GLMM for female condition scores, comparing lactating versus dry females, controlling for individual and month.

Variable	F Statistic	df	p*
Whole year (October 2005 – May 2006)			
Full model§	0.34	9,214	0.458
Lactating vs dry	1.43	1,214	0.117
Month	0.31	8,214	0.481
Estimated marginal means: lactating = 2.90; dry = 2.86			
Pregnancy (October-December)			
Full model§	0.55	4,93	0.350
Lactating vs dry	0.40	1,93	0.265
Month	0.60	3,93	0.308
Estimated marginal means: lactating = 2.95; dry = 2.92			
Lactation (January-March)			
Full model§	0.24	3,70	0.433
Lactating vs dry	0.49	1,70	0.245
Month	0.12	2,70	0.445
Estimated marginal means: lactating = 2.87; dry = 2.82			
Post-weaning (April-May)			
Full model§	0.61	5,115	0.347
Lactating vs dry	0.56	1,115	0.229
Month	0.63	4,115	0.322
Estimated marginal means: lactating = 2.92; dry = 2.89			

* 1-tailed test of a specified a priori directional hypothesis

§ Full model controlling for individual and month

Figure 1

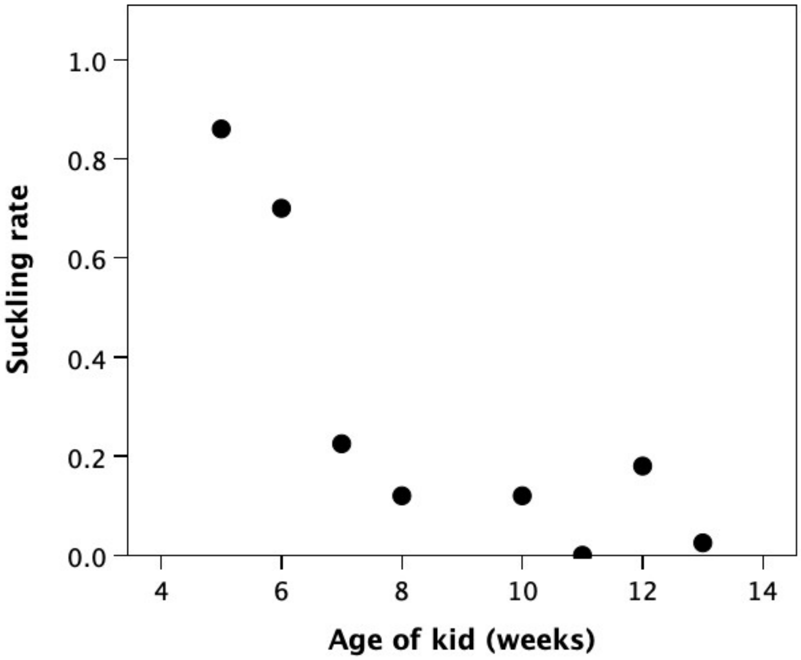


Figure 2

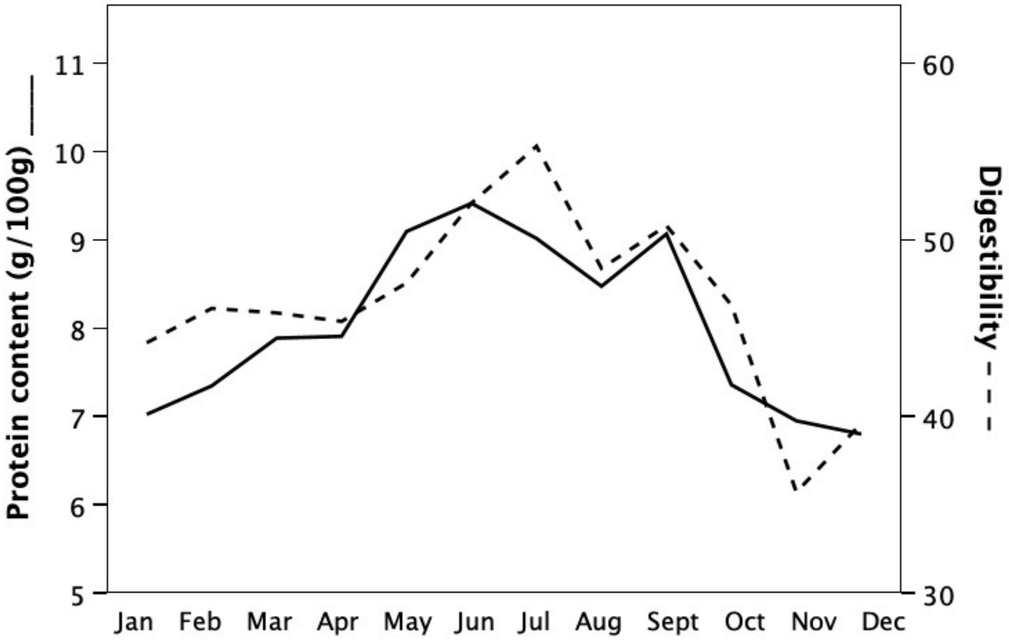

Protein content (g/100g) ____
Digestibility - - -
11
10
9
8
7
6
5
60
50
40
30
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec

Figure 3

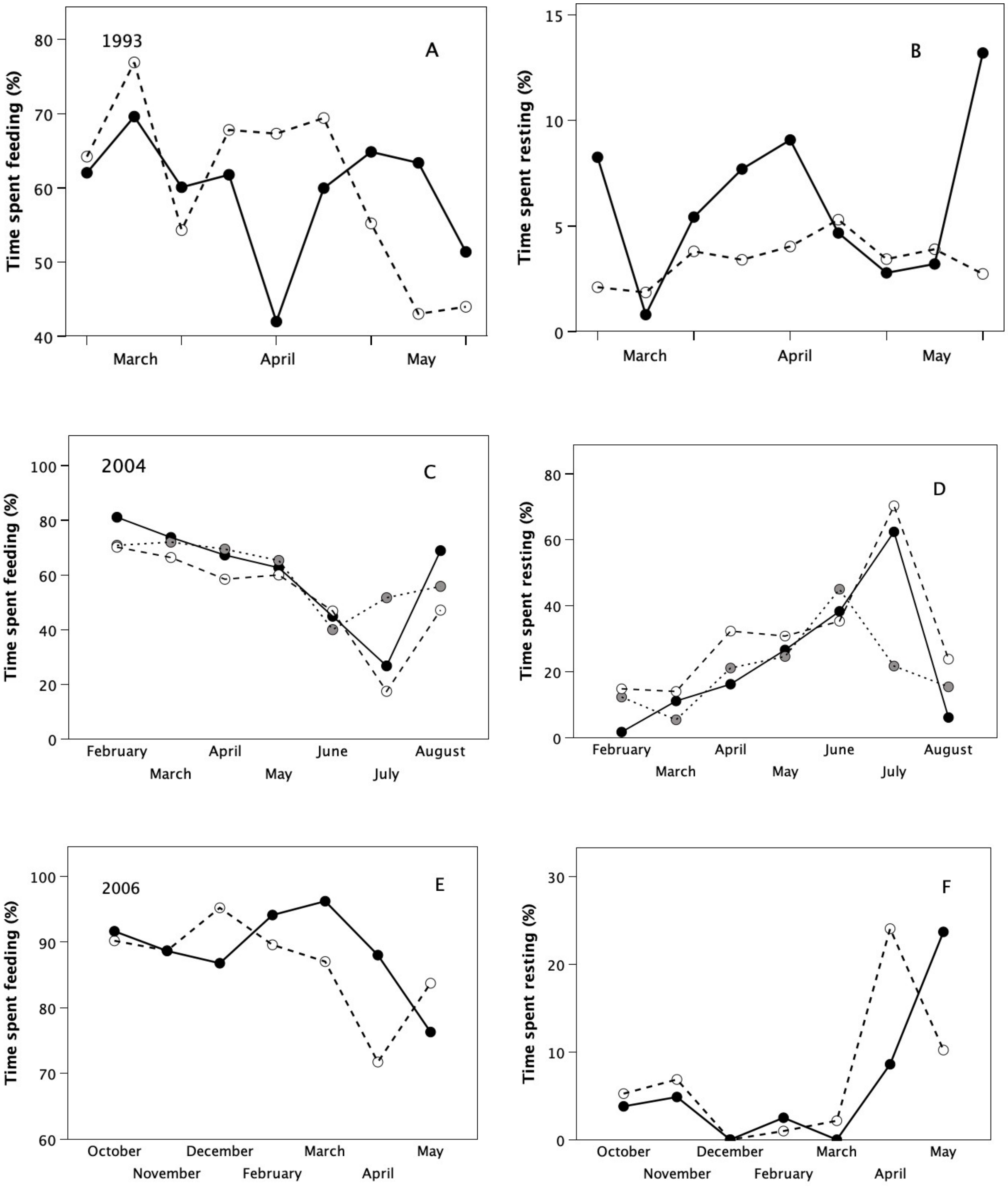

1993
A
Time spent feeding (%)
40
50
60
70
80
March
April
May
B
Time spent resting (%)
0
5
10
15
March
April
May
2004
C
Time spent feeding (%)
0
20
40
60
80
100
February
March
April
May
June
July
August
D
Time spent resting (%)
0
20
40
60
80
February
March
April
May
June
July
August
2006
E
Time spent feeding (%)
60
70
80
90
100
October
November
December
February
March
April
May
F
Time spent resting (%)
0
10
20
30
October
November
December
February
March
April
May

Figure 4

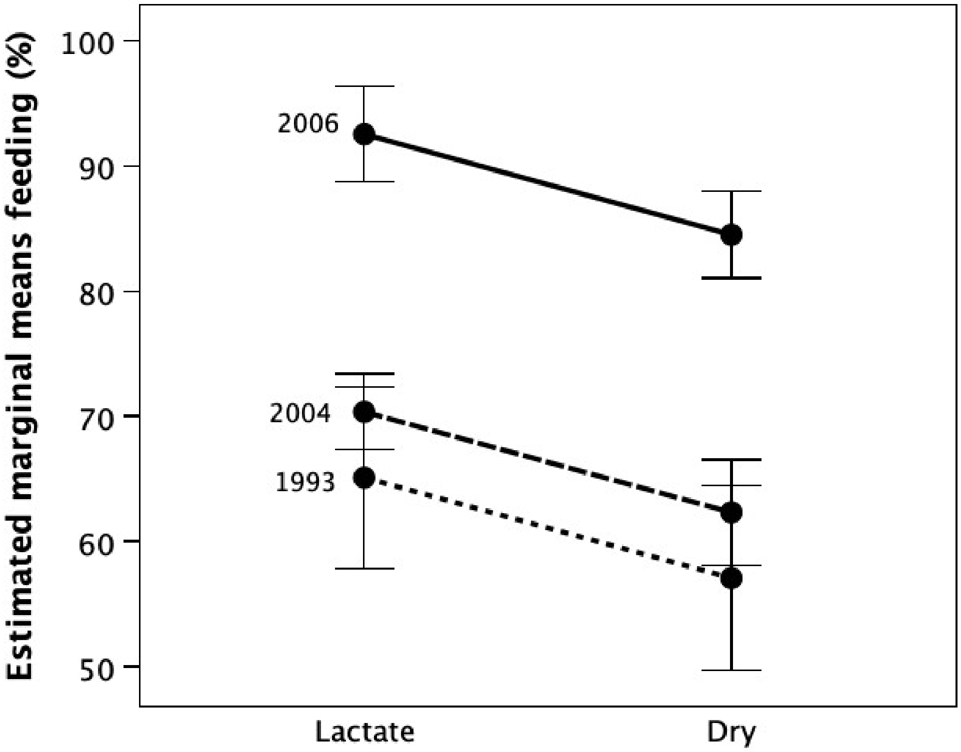

Estimated marginal means feeding (%)
100
90
80
70
60
50
2006
2004
1993
Lactate
Dry

Figure 5

Figure 6

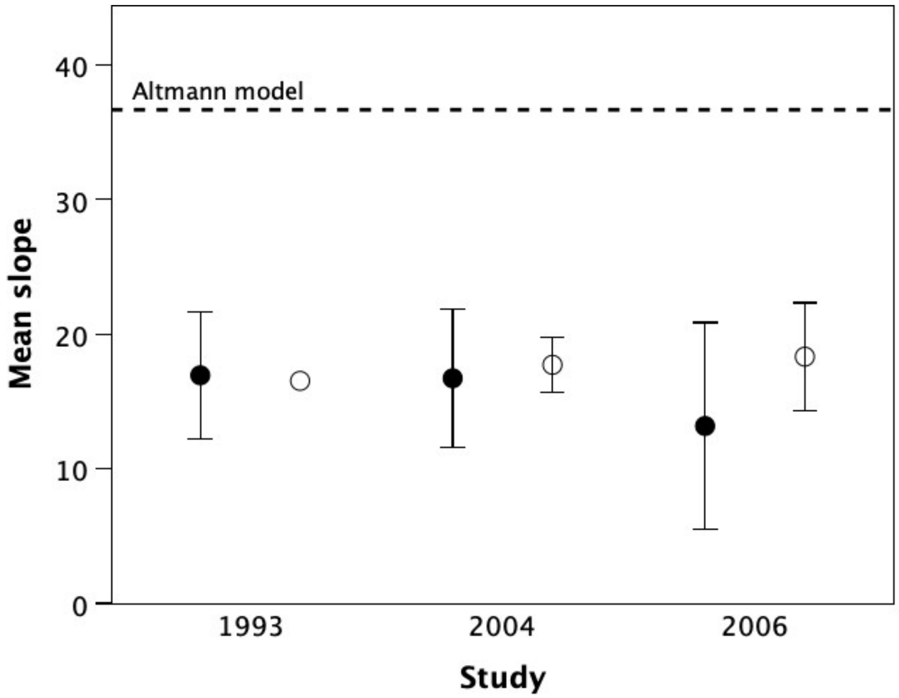


Figure 7

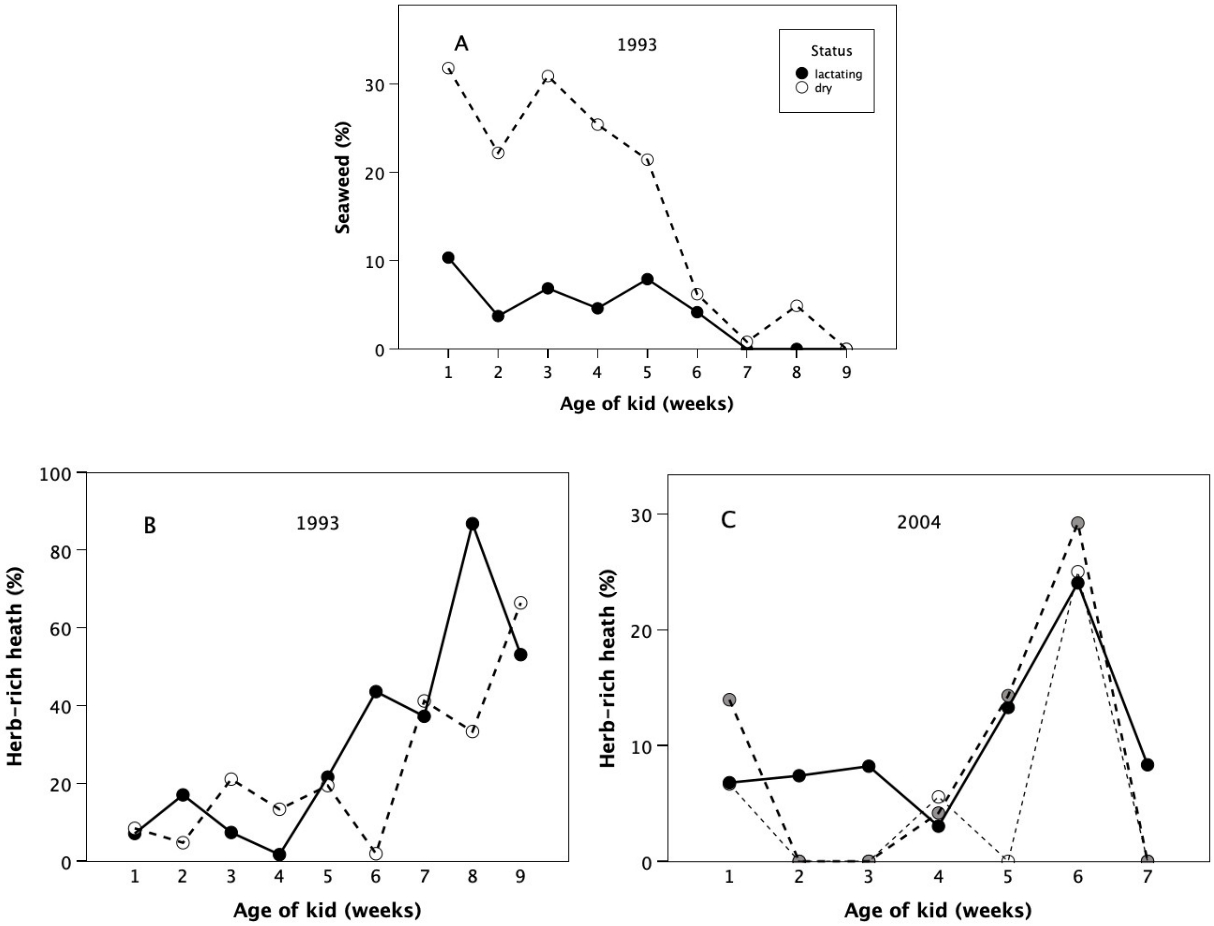

A
1993
Status
lactating
dry
Seaweed (%)
0
10
20
30
1
2
3
4
5
6
7
8
9
Age of kid (weeks)
B
1993
Herb-rich heath (%)
0
20
40
60
80
100
1
2
3
4
5
6
7
8
9
Age of kid (weeks)
C
2004
Herb-rich heath (%)
0
10
20
30
1
2
3
4
5
6
7
Age of kid (weeks)

Figure 7 (contd)

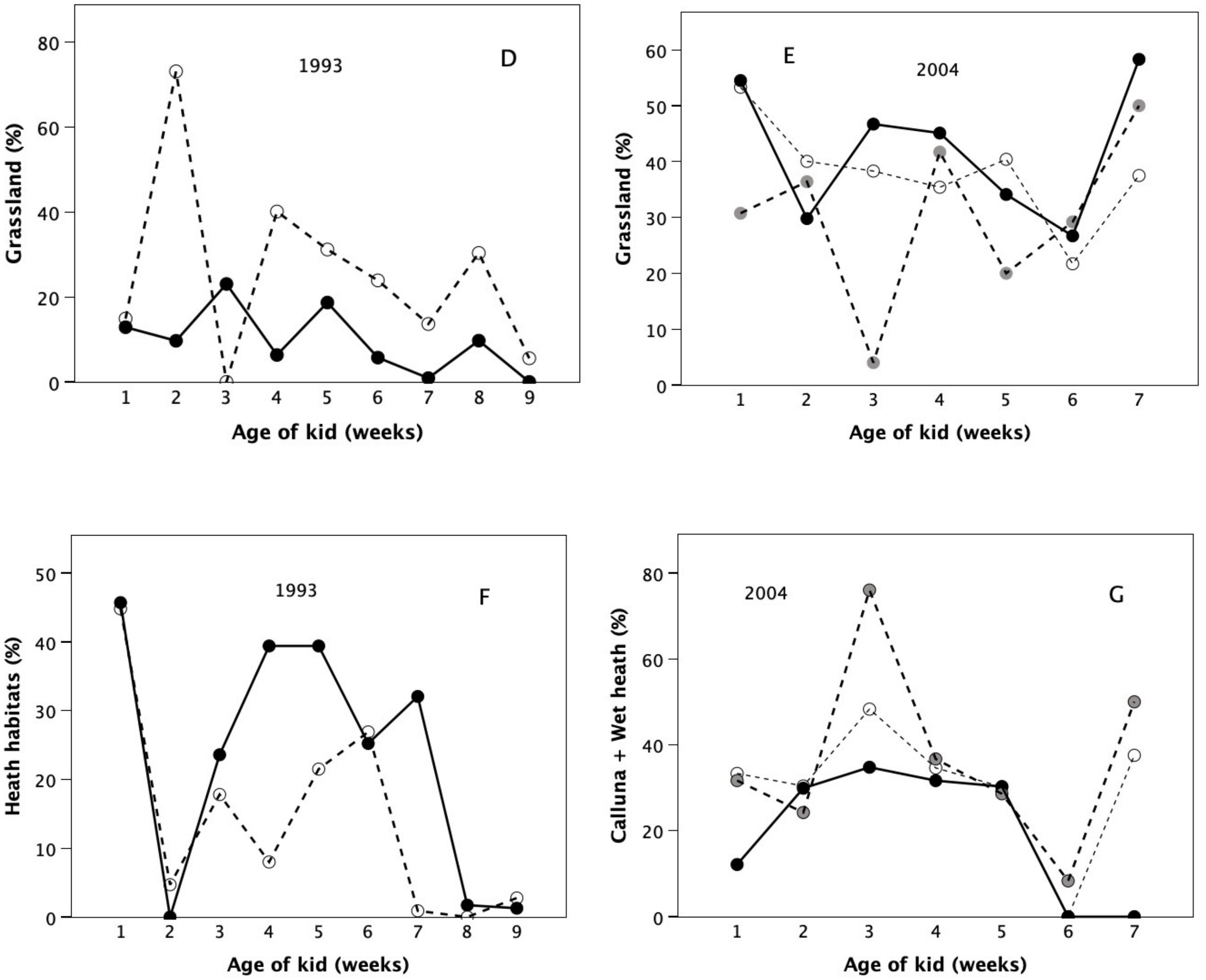


Figure 8

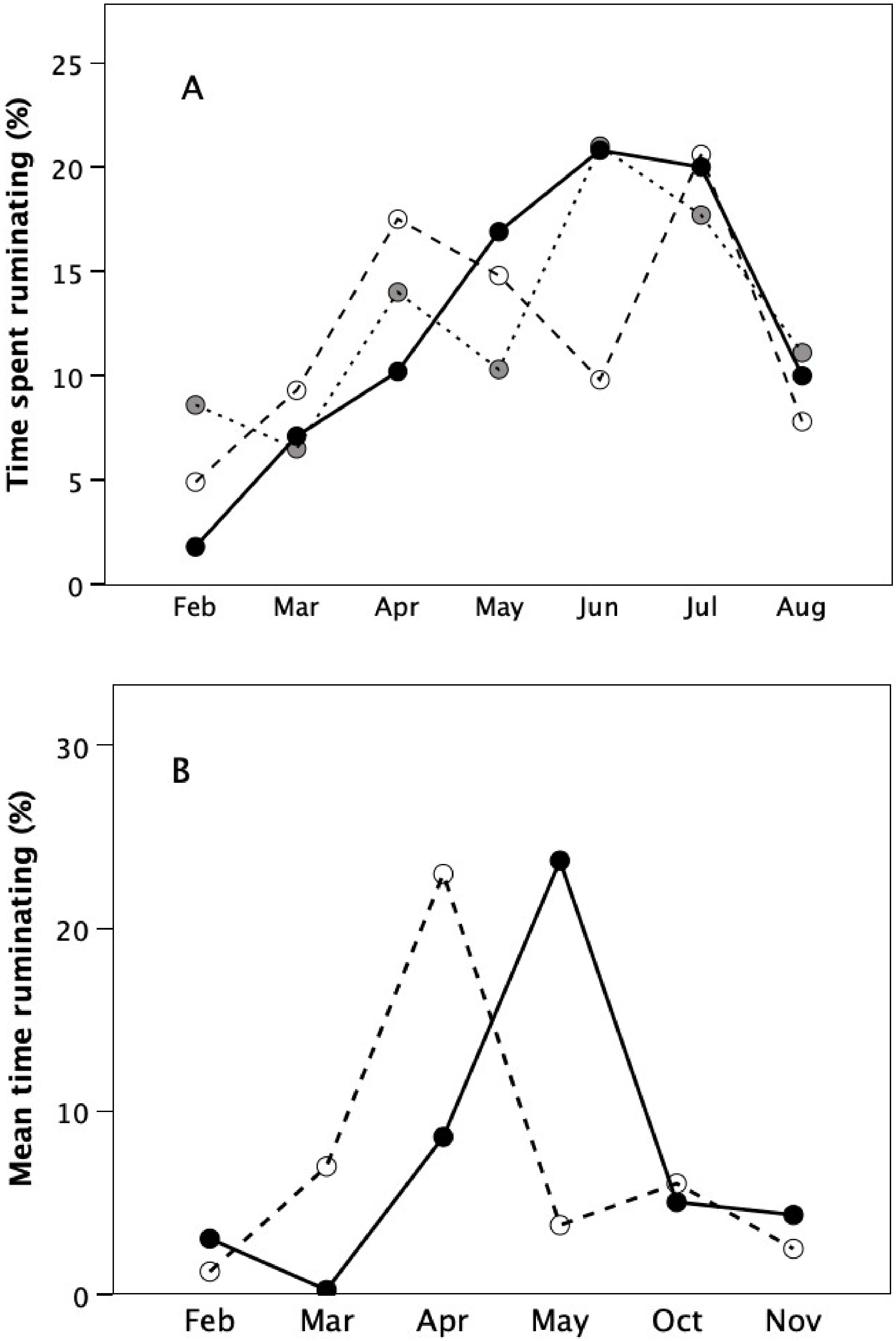
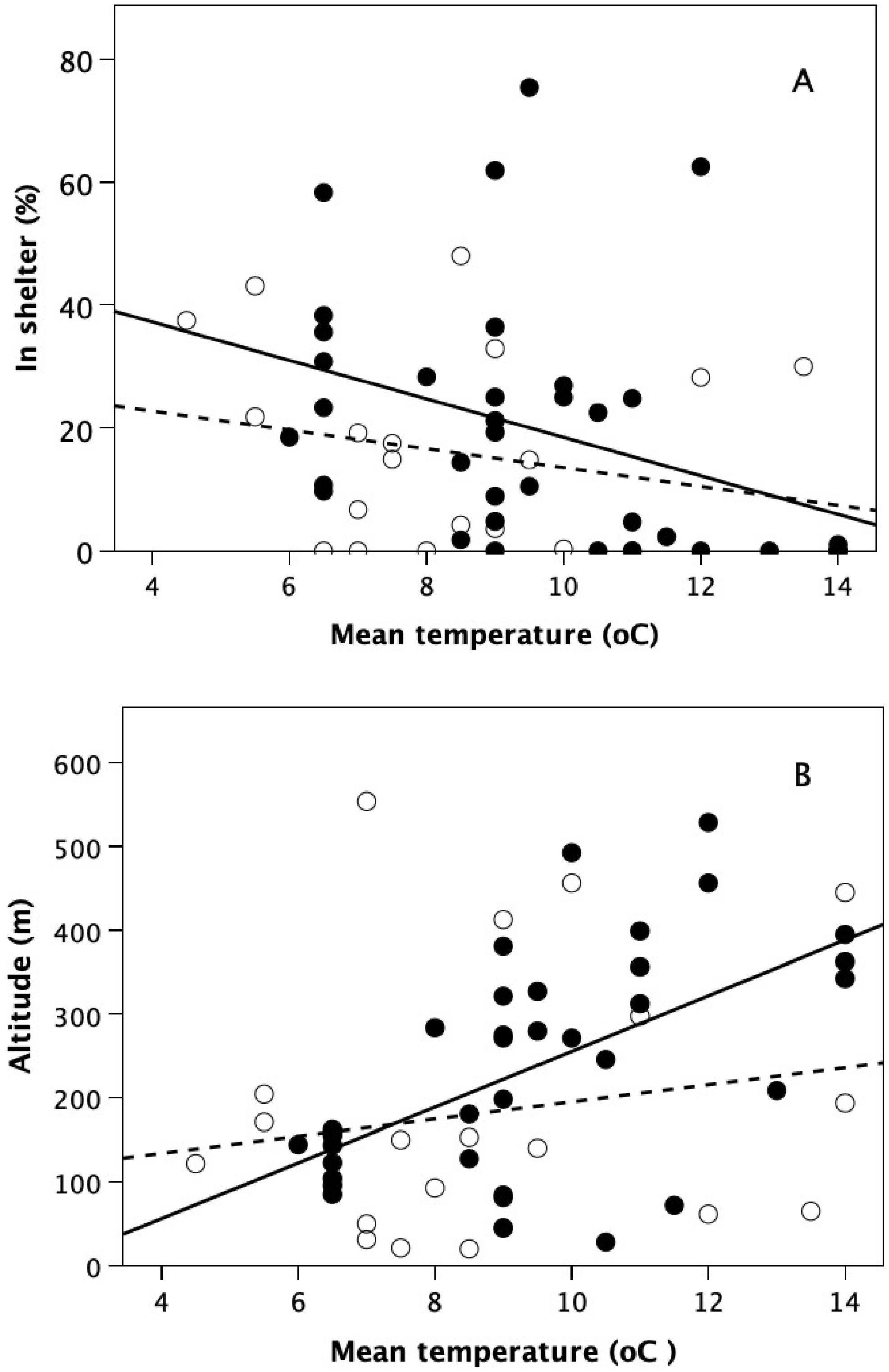
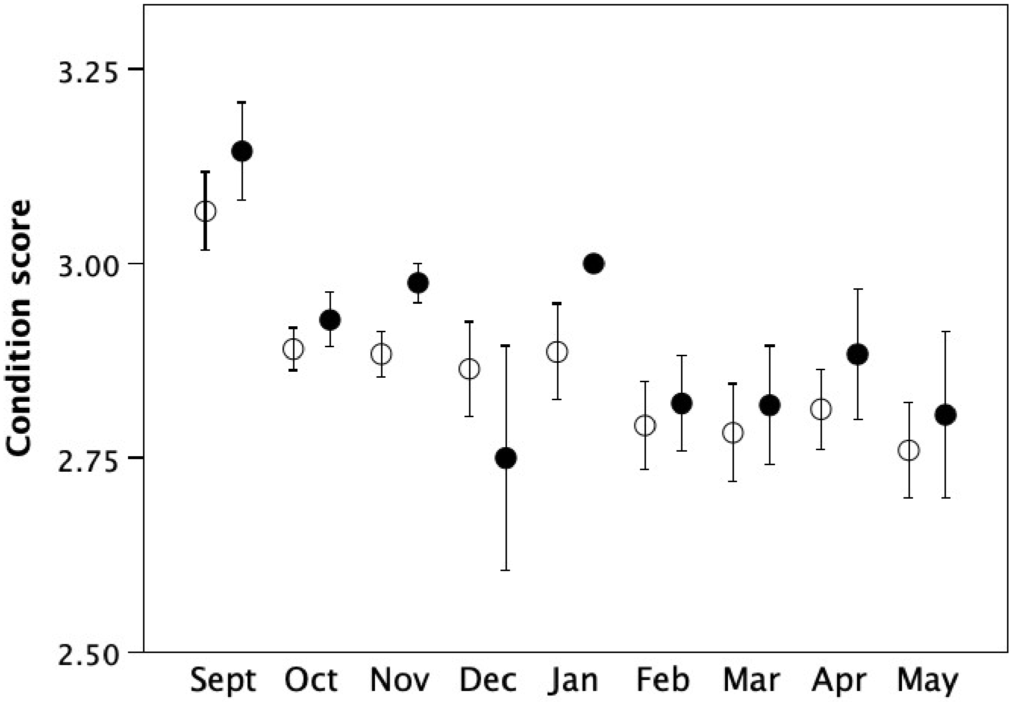

A
Time spent ruminating (%)
0
5
10
15
20
25
Feb
Mar
Apr
May
Jun
Jul
Aug
B
Mean time ruminating (%)
0
10
20
30
Feb
Mar
Apr
May
Oct
Nov

Figure 9


A
In shelter (%)
0
20
40
60
80
4
6
8
10
12
14
Mean temperature (oC)
B
Altitude (m)
0
100
200
300
400
500
600
4
6
8
10
12
14
Mean temperature (oC)

1025

Figure 10



Condition score
3.25
3.00
2.75
2.50
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May

Figure 11

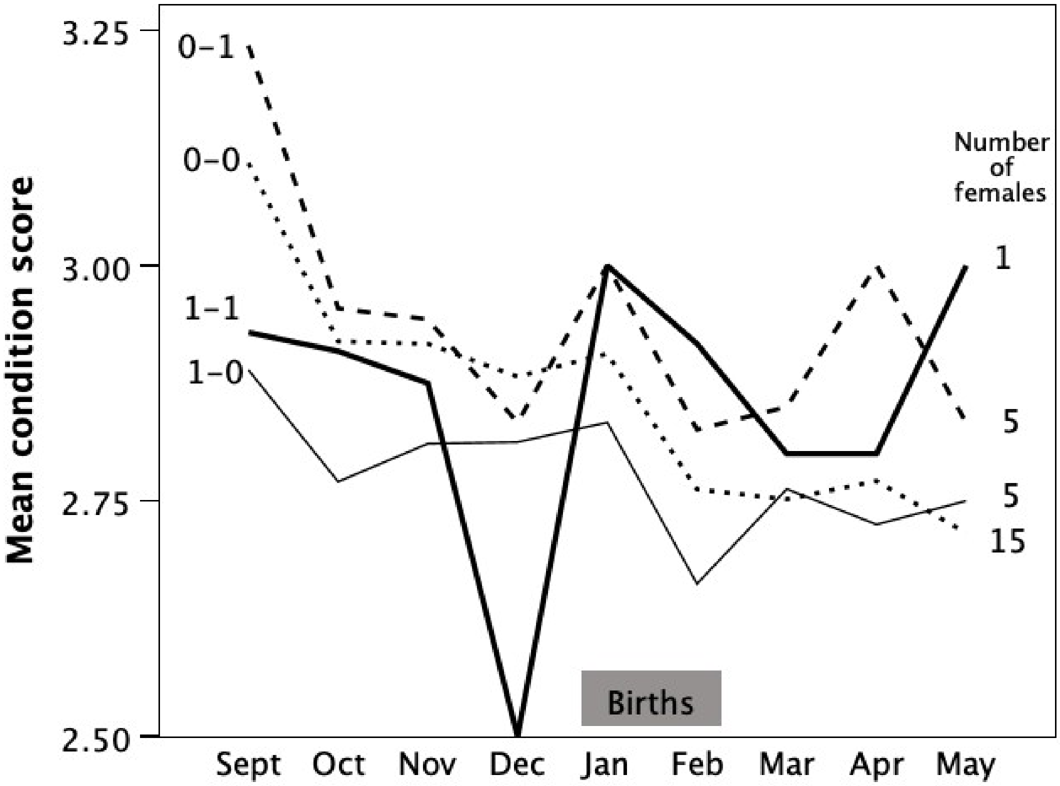

3.25
3.00
2.75
2.50
Mean condition score
0–1
0–0
1–1
1–0
Number of females
1
5
5
15
Births
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May

Figure 12

Figure 13