The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species

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Abstract

The range-shifts of many species are lagging behind climate change, meaning that those species are likely to experience increases in average ambient temperature. Heat-sensitive species may experience increasingly precarious trade-offs between investment in thermoregulation versus other key processes as the climate warms. We investigated the potential for trade-offs to exist between behavioral thermoregulation and foraging, studying a typical heat-sensitive endotherm: the Alpine ibex (*Capra ibex*). Ibex use higher altitudes when it is hotter, which could restrict them from more profitable foraging areas at lower altitudes. We investigated this potential trade-off using data on the altitude-use and activity budgets of 43 marked males collected during the vegetation growing season in Gran Paradiso National Park, Italy. We used structural equation modeling to assess the support for models linking ambient temperature, altitude-use, vegetation productivity and foraging time. Ibex migrated to higher altitudes during spring and summer, maintaining their ambient temperature within a very narrow band. Consequently, when it was warmer ibex utilized areas that were less productive, as indicated by lower normalized difference vegetation indices, and consumed lower quality forage, as indicated by lower levels of fecal crude protein. Ibex did not compensate behaviorally for reduced forage productivity by adjusting their foraging effort. We identify a trade-off between thermoregulation and foraging in ibex, which could affect this species negatively in the future. Such trade-offs could be a general phenomenon for heat-sensitive species. Our study reveals that behavioral thermoregulation can exert a strong influence on animal distributions, even overriding resource productivity in importance.

Key words: Alpine ibex, behavioral thermoregulation, climate change, foraging, trade-off, ungulate.

Introduction

Global average surface temperatures increased by 0.85°C between 1880 and 2012, and are likely to rise by a further 1.0-3.7°C by the end of this century (IPCC, 2013). Many species are responding to this warming by shifting their spatial distributions poleward and to higher altitudes in order to remain in climatically suitable areas (Parmesan and Yohe, 2003). In general, however, range-shifts – and in particular altitudinal shifts – are lagging behind climate change, with species likely experiencing higher mean environmental temperatures as a result (Chen et al., 2011; Menéndez et al., 2006). Increasingly, researchers are considering the physiological implications of such temperature increases (e.g., Chown et al., 2010; Helmuth, 2009) and it is becoming clear that rising temperatures will strongly affect animal species' energy and water balances unless mechanisms exist with which to buffer against them (Boyles et al., 2011). The adaptation of autonomic and behavioral thermoregulation is predicted to play a key role in the response of many species to climate change (Boyles et al., 2011; Huey et al., 2012; Kearney et al., 2009). However, increasing investment (i.e., time and energy) in thermoregulation reduces the resources available for other key processes such as growth and survival (Dunbar, 1998; Kearney and Porter, 2004). As the climate warms, species may face increasingly precarious trade-offs between investment in thermoregulation and other processes.

Heat-sensitive endotherms may be particularly affected by increasing temperatures due to their high energetic and water requirements. Endotherms must expend large amounts of energy and water to regulate metabolic heat production when experiencing environmental temperatures outside of their preferred range (McNab, 2002). Repeated exposure to elevated temperatures can negatively affect endotherm body condition and survival (Gardner et al., 2016), while short periods of extreme temperatures can cause mass die-offs (McKechnie et al., 2012; Welbergen et al., 2008). Heat-sensitive endotherms may be largely reliant on responding to climate change using behavioral thermoregulation, which is thought to be less energetically expensive than autonomic thermoregulation (Terrien et al., 2011). Endotherms exhibit a diverse array of behavioral strategies to buffer themselves against environmental temperature fluctuations. In high temperatures, species may employ heat-dissipating behaviors, such as posturing (du Plessis et al., 2012; Stelzner and Hausfater, 1986), and may have activity rhythms entrained to temperature fluctuations, being less active when it is warmer (Brivio et al., 2016; Mason et al., 2014b). Additionally, mobile endotherms may select cooler microclimates in their environment, ranging from using cooler habitat types (Marchand et al., 2015) to cooler areas within these habitats, such as shaded areas under trees or rocks (Mysterud and Østbye, 1999). It is well understood that investment in behavioral thermoregulation requires animals to devote time and energy away from other key behaviors (Dunbar, 1998; Kearney and Porter, 2004). The selection of thermally suitable microclimates may have an additional cost, by driving animals away from areas favorable in terms of resource productivity or predation risk. This could lead to lower rates of resource acquisition or survival, reducing fitness even when animals are not actively performing thermoregulatory behaviors. To date, studies of such trade-offs have mainly been restricted to those between thermoregulation and survival. For instance, species may trade off habitat thermal suitability against predation risk (Marchand et al., 2015). However, an understanding is growing of a potential trade-off between microclimate selection and resource acquisition, which could have an important bearing on species' energy budgets (van Beest et al., 2012). Such trade-offs are likely to have implications for how species respond to climate change. Quantifying these trade-offs in current climatic conditions is an important first step to understanding how they may be affected by future warming.

For large herbivores, habitat use and selection are thought to be influenced primarily by trade-offs between resources and predation-risk (Sih, 1987). However, thermoregulation can also exert an important influence on their distributions (see Mysterud and Østbye, 1999), as has been demonstrated for heat-sensitive and tropical species (van Beest et al., 2012; Wiemers et al., 2014). Here, we investigate a potential trade-off between behavioral thermoregulation and foraging in a heat-sensitive herbivore, the Alpine ibex (*Capra ibex*), during the vegetation growing season (May-October) – the critical period for mountain ungulates to acquire energy prior to the rigors of winter (Büntgen et al., 2014; Giacometti et al., 2002; Pettorelli et al., 2007). Ibex are a cold-adapted species reliant on behavioral mechanisms to cope with high temperatures during the spring and summer, and can experience heat discomfort and stress above ambient temperatures of 15°C (Aublet et al., 2009; Grignolio et al., 2004). Ibex cope with high temperatures during spring and summer predominantly through reductions in activity and by moving to higher altitudes (Aublet et al., 2009). Ibex may experience lower forage biomass and quality at higher altitudes, where alpine meadows are less common, and more sparsely vegetated areas predominate (Aublet et al., 2009). As such, ibex foraging behavior during spring and summer could be shaped by a trade-off between thermoregulation and energy acquisition. In order to understand how such a trade-off could affect ibex under climate change, it is necessary to consider whether they can mitigate against it. For ibex, which have activity budgets entrained to seasonal environmental variation (Aublet et al., 2009; Signer et al., 2011), this could entail adjustments to the proportion of time devoted to foraging as a function of forage productivity.

We examined the altitudinal response of ibex to variation in ambient temperature and investigated how this shapes their thermal and foraging environment. We evaluated support for an indirect causal pathway between temperature, altitude, vegetation productivity and time spent foraging (see Fig. 1), using the Normalized Difference Vegetation Index (NDVI) as a proxy for vegetation productivity. We tested two main hypotheses: 1) ibex experience reduced NDVI at higher temperatures due to migration to higher altitudes, and 2) ibex compensate behaviorally for altitude-driven NDVI reductions by adjusting their time spent foraging. We define behavioral compensation as the use of behaviors that reduce the energetic cost of a given ecological process. Ibex may compensate behaviorally by foraging for longer, in either i) high NDVI areas, to make use of their limited time there, or ii) low NDVI areas, to deal with low forage productivity in these areas. Finally, by analyzing data collected on the protein content of fecal samples, we assessed whether any identified predictors of foraging area NDVI were also related to the quality of ingested forage. Using our results, we evaluated the potential importance of thermoregulation-foraging trade-offs for understanding the responses of ibex, and thermally sensitive species in general, to climate change.

Methods

Study area

We conducted the study in the Levionaz valley (1700 ha) of Gran Paradiso National Park in the North-Western Italian Alps (45°35’ N, 7°12’ E). The study area consists of steep glacial valleys, ranging from 1,650 to 3,300 m a.s.l., characterized by alpine meadows (predominantly consisting of *Festuca varia*), moraines, rock cliffs and glaciers. The local climate is temperate, with snowfall mostly occurring between

November and April. The warmest period of the year occurs between June and September. Levionaz valley contains a population of Alpine ibex that are monitored as part of a long-term study of behavioral and population ecology. During our study, 151 ibex were recorded in Levionaz by the annual autumn census (60 males, 58 females, 13 yearlings and 20 kids; for further details see Jacobson et al. 2004). Ibex are captured and marked each year in Levionaz, between April and September, by park wardens and veterinarians. At capture, ibex are aged by counting horn annuli (von Hardenberg et al., 2004) and fitted with individually recognizable colored ear-tags or collars (see Brivio et al. (2015) for further details). During our study there were 45 marked males in Levionaz, aged 2-15 years. Hunting of ibex is not permitted in the park. During the study period, a pack of grey wolves (*Canis lupus*) was present in the park, which preyed predominantly on Alpine chamois (*Rupicapra rupicapra*), the only other mountain ungulate in the study area (Palmegiani et al. 2013). Ibex made up a small proportion of the pack's diet (8-9% during summer).

Data collection

We monitored male ibex behavior between May and October 2011. We focused on males because they are easier to locate and observe over long periods than females, which are accompanied by young kids at this time of year. We selected marked males and continuous focal observations were conducted by single observers using binoculars and spotting scopes (Martin and Bateson, 1993). Ibex were observed from distances >200 m to ensure that observer presence did not influence ibex behavior. To construct individual activity budgets, any changes in behavioral state maintained for over 1 minute were recorded for the following behaviors: foraging, lying, moving, standing, social activity, and other (see Brivio et al. (2010) for detailed definitions). Ibex devoted most time to lying (46%) and foraging (43%) during daylight hours (Supplementary

Fig. S1). The duration of focal observations depended on weather conditions, varying between 45 and 420 minutes (mean 257 minutes). Observation sessions were uniformly distributed over daylight hours (05:40 - 21:30) and across individuals, ensuring that each marked male was sampled every 2–3 weeks. A total of 374 observations (across 1,610 hours) were performed across 43 ibex, distributed evenly throughout the study period.

Ibex locations were recorded at the beginning and the end of each observation period by identifying their locations on a 1:25,000 scale map. To investigate the influence of environmental factors on ibex foraging behavior, we quantified the environmental conditions for the mean location per observation. We derived the altitude, aspect and slope of locations using a 10 m resolution Digital Elevation Model of the European Alps provided by the Regione Autonoma Valle d'Aosta. We quantified the vegetation productivity of locations using NDVI derived from Moderate-resolution Imaging Spectroradiometer (MODIS) data processed by the Earth Resources Observation and Science Center (http://glovis.usgs.gov/). These data are at a 250 m spatial resolution and are available at 16-day intervals. To account for variation in NDVI occurring solely driven by seasonal vegetation maturation and senescence, we calculated ΔNDVI: the difference between the NDVI of an ibex's location and the mean NDVI of the study area at a given time-step. To calculate mean study area NDVI we defined the area used by ibex during the study period as the 100% minimum convex polygon of all ibex locations, removing an enclosed area of bare rock and snow higher than 3,100 m, as it contained no suitable ibex habitat. We calculated mean NDVI within this area for each time-step, weighted by the proportion of each 250 x 250 m NDVI pixel within the area. ΔNDVI thus represented the productivity of a location relative to other areas of suitable habitat available at that time in the study area. To investigate the influence of temperature on the altitude of areas used by ibex (hereafter called "ibex altitude") and their time spent foraging, we used mean daily ambient temperature (hereafter, 'mean daily temperature'). Hourly temperature data were recorded at a resolution of 0.1°C by a digital data-logger, protected from solar radiation, at an automatic weather station located in the study area at 1,951 m (45°31.33' N, 7°12.6' E; Meteorological Service of Regione Autonoma Valle d'Aosta). We averaged the hourly temperature data recorded during daylight hours to produce mean daily temperature.

Finally, we collected data on the proportion of crude protein in ibex fecal samples to determine the relationship between NDVI and forage quality. Fecal crude protein content (hereafter, 'FCP') is a reliable indicator of the quality of ingested forage (Leslie and Starkey, 1985) and has been used widely in the study of wild ungulates (e.g., *Capreolus capreolus*: Kamler & Homolka 2005; *Cervus elaphus*: Hebblewhite, Merrill & McDermid 2008; *Ovis canadensis*: Festa-Bianchet 1988). We collected fresh fecal samples from marked male ibex at the start of each month, using binoculars to observe individuals defecating, and collecting fecal samples immediately after ibex had moved away. The time between defecation and collection was always less than 20 minutes. We did this for as many marked ibex as possible each month. We stored samples in plastic bags at -20°C, prior to drying them and analyzed their crude protein content (Nitrogen x 6.25) using the macro-Kjeldhal acid digestion technique (Kjeldahl, 1883). We characterized the environmental conditions (altitude, aspect, slope and NDVI) corresponding to each sample based on observations of individuals in the 1-4 days prior to the observed defecation. In a related species, the Nubian ibex (*Capra nubiana*), the mean retention time of vegetation in the digestive tracts of adult males is 28-57 hours, depending on particle size (Gross et al., 1996). Focusing on the 1-4 day period (i.e., 24-96 hours) prior to defecation provided a snapshot of the NDVI experienced by ibex while foraging on the vegetation contained within fecal samples, allowing for variation around mean digestion time. We collected 67 samples from 30 individuals (aged 2-15 years) with associated environmental data.

Statistical methods

Prior to fitting models it was necessary to assess whether NDVI was a suitable proxy for the quality of forage consumed by ibex. We did this by performing a Pearson's correlation test between the mean FCP and NDVI of each ibex for which there were FCP data ($n = 30$). FCP and NDVI are significantly positively correlated, indicating that ibex consumed higher quality forage in higher NDVI areas (Pearson's r: 0.46; 95% CIs: 0.13 - 0.71; $P < 0.01$; Supplementary Fig. S2).

We used structural equation modeling (SEM), a multivariate modeling approach that evaluates the overall fit of a hypothesized network of linked models (Grace, 2006). SEMs are represented by path diagrams in which arrows represent hypothesized causal relationships and variables can appear as both predictors and responses (see Fig. 1). This approach is appropriate here as it allowed us to assess support for the indirect causal pathway between temperature, altitude, ΔNDVI and time spent foraging as a whole, rather than examining the direct drivers of different response variables individually. We considered the hypothesized SEM displayed in Figure 1 as our maximal model. Since classical SEM approaches cannot incorporate random effects, which are necessary to analyze individually-structured data, we adopted a piecewise approach, first fitting separate linear mixed-effects models with individual-level random intercepts, before combining these in a SEM. We tested models for: i) altitude, ii) ΔNDVI and iii) time spent foraging. We fitted models using maximum likelihood, implemented with the ‘lme’ function of the ‘nlme’ R package (Pinheiro et al., 2014). We evaluated the distributions of model residuals to ensure that assumptions of normality were not violated.

For the altitude model we considered three predictors: mean daily temperature, time of day and ibex age. We used the midpoint of each observation to represent time of day. We considered a quadratic effect of time because ibex exhibit daily movements between different altitudes, tending to use higher altitudes in the middle of the day (Aublet et al., 2009). We considered age because altitude-use may vary with body size (Aublet et al., 2009), due to higher thermal sensitivity (Peters, 1986) or different energy requirements (Demment and Van Soest, 1985) of larger individuals. Male ibex mass varies substantially with age; they reach asymptotic mass at 9-10 years, when they weigh on average 1.5 times that of 5 year old (Bergeron et al., 2010). For the ΔNDVI model, we considered effects of altitude, aspect, slope and ibex age. Age may again play a role because different energy requirements of larger individuals could influence the type of vegetation on which they forage (Brivio et al., 2014), affecting ΔNDVI independently of altitude. We included aspect and slope to account for variation in vegetation productivity driven by topography. We used the cosine of aspect to investigate differences in ΔNDVI between northerly and southerly facing slopes, which are likely to vary in sun and wind exposure. For the time spent foraging model, we considered effects of ΔNDVI, time of day, mean daily temperature, aspect, slope and ibex age. We considered ΔNDVI, aspect and slope to test whether ibex adjusted their time spent foraging depending on vegetation productivity and general foraging conditions. We considered a quadratic time of day effect, as ibex spend more time foraging in the morning and evening, and a linear temperature effect, as ibex spend less time foraging on hotter days (Aublet et al., 2009). Additionally, we considered an interaction between these effects to assess whether the influence of time of day on foraging varied with temperature. We considered age because large males may spend less time foraging due to lower relative energy needs (Aublet et al., 2009).

We scaled variables prior to modeling ($[x - \bar{x}]/\sigma_x$) to produce standardized coefficients, comparable among predictors. For each model, we considered all possible combinations of predictors, and assessed model parsimony using Akaike's Information Criterion (AIC). We considered models with ΔAIC ≤6 as candidate sub-models for SEMs (Richards, 2008). Next, we combined the candidate sub-models of altitude, ΔNDVI and time spent foraging into SEMs. We considered different candidate SEMs depending on the interdependence of candidate sub-model sets. In total we considered 72 models, 8 of which linked only the altitude and ΔNDVI sub-models (see Supplementary Table S1). We assessed SEM model fit using directional separation tests (Shipley, 2009), implemented with the 'piecewise.sem' R package (Lefcheck, 2015). Directional separation tests calculate the statistical significance of potential causal paths missing from the fitted model (only considering variables already in the model), producing an overall measure of model fit: Fisher's *C* statistic. Models with Fisher's *C* statistic $P > 0.05$ are considered to represent the underlying data adequately. We retained the SEMs that represented the data adequately and compared their performance with AIC calculated using Shipley's (2013) method based on Fisher's *C* statistic. We considered models with ΔAIC ≤6 and lower than that of all simpler nested models to have some support (Richards, 2008). To examine the performance of the best SEM, we plotted the partial effects between response variables and key predictors. Partial effect plots display relationships between a response and predictor, while accounting statistically for the effects of other predictors in that model (for further details see Lefcheck, 2015).

Next, we examined whether any proximal drivers of reductions in ΔNDVI were associated similarly with FCP. We fitted linear mixed-effects models using ‘lme’ with FCP as the response variable and all tested proximal drivers of ΔNDVI as predictors (i.e., age, altitude, aspect and slope). We used independent random intercepts for individual and day of year. Day of year random effects were included to account for seasonal changes in vegetation protein content occurring due to vegetation maturation and senescence. Due to the relatively low sample size of the FCP data ($n = 67$), we used AICc rather than AIC for model selection. As above, we considered models with ΔAICc ≤6 and lower than that of all simpler nested models to have some support (Richards, 2008).

Finally, we explored seasonal temporal trends in temperature, altitude and NDVI to illustrate the effects of the causal pathway identified using SEM on the environmental conditions experienced by ibex over the season. We fitted linear mixed-effects models for i) altitude, ii) temperature and iii) NDVI experienced by ibex, with day of year as a predictor and individual-level random intercepts. For temperature experienced by ibex, we used temperature data recorded at survey locations using iButton data-loggers (iButton Temperature Loggers DS1921G-F5, Maxim Integrated; resolution 0.5°C). Loggers were placed 1 m above ground level, within a white perforated box to protect them from solar radiation. For comparison, we then fitted trends for i) mean daily temperature and ii) mean daily study area NDVI. Here, we considered NDVI, rather than ΔNDVI, to visually compare the seasonal trends in NDVI experienced by ibex with trends in NDVI of the study area. We considered models with linear, quadratic or no trends, identifying the most parsimonious option with AIC (see Supplementary Table S2).

Results

We find strong evidence for the indirect causal pathway between temperature, altitude and ΔNDVI experienced by ibex, and thus for a trade-off between thermoregulation and access to forage (Fig. 2a; Tables 1 & 2). However, there is no evidence that ibex compensated behaviorally for this trade-off by adjusting their time foraging depending on forage productivity.

There is a strong positive relationship between mean daily temperature and ibex altitude (Table 1a; Fig. 2b). Mean daily temperature shows an increasing quadratic temporal trend, from 7.4°C in May up to 13.4°C in August (1st), before decreasing to 7.6°C by late October (Fig. 3a). Mean ibex altitude shows a similar quadratic trend, increasing during spring and summer, from around 2,200 m in May, peaking in August (9th) at over 2,770 m, before decreasing to around 2,400 m by late October (Fig. 3b). There is considerable support for a strong, positive effect of mean daily temperature on ibex altitude, suggesting that the observed pattern of seasonal ibex altitudinal migration was driven by seasonal temperature variation. Both candidate altitude models contain an effect of temperature and strongly outperformed the null model according to AIC (Table 1a). As with mean daily temperature, the temperature experienced by ibex shows a quadratic seasonal trend, but this effect is much less pronounced (Fig. 3a). The temperatures ibex experienced increased slightly from 7.1°C in May to 9.6°C in August (6th), decreasing to 7.7°C by late October. Despite the mean daily temperature trend varying by 6°C, the mean trend in temperature experienced by ibex varies by only 2.4°C, suggesting that altitudinal migration buffered ibex against environmental temperature variation. Both candidate altitude models also contain weaker, negative effects of age, suggesting that older ibex tended to use lower altitude areas (Table 1a).

Ibex altitude strongly influenced ΔNDVI, the NDVI experienced by ibex relative to the mean NDVI of the study area. Mean study area NDVI displays an increasing quadratic trend, being lowest (0.1) in May, peaking at 0.37 in August (19th) and decreasing slightly to 0.27 by late October (Fig. 3c). In contrast, the mean NDVI experienced by ibex shows the reverse quadratic trend, being highest (0.33) in May, before decreasing to 0.25 in August (11th) and increasing to 0.3 by late October. As such, ibex experienced highest NDVI early in the season, at a time when the overall NDVI of the study area was lowest. Ibex experienced slight reductions in NDVI throughout the season, despite the mean NDVI of the study area increasing substantially during spring and summer. There is strong evidence that reductions in ΔNDVI experienced by ibex were due to altitudinal migration: there is considerable support for a strong, negative effect of ibex altitude on ΔNDVI (Table 1b; Fig. 2c). All candidate ΔNDVI models contain strong effects of altitude and weaker, positive effect of aspect. The aspect effect suggests that ibex experienced higher NDVI relative to the study area average when on northerly facing slopes. The candidate models strongly outperform the null model according to AIC.

There is only weak evidence from the mixed-effects models that ibex adjusted their time spent foraging depending on ΔNDVI (Table 1c). Time spent foraging was influenced predominantly by time of day, mean daily temperature and an interaction between the two; both predictors and their interaction are present in all candidate foraging models. There is a strong quadratic effect of time of day, with ibex spending more time foraging in the morning and evening (Fig. 4), and a weaker negative effect of temperature, with ibex foraging less on warmer days. Additionally, the interaction between these predictors indicates that ibex spent more time foraging in the morning and less time foraging in the evening of warmer days (Fig. 4). Eight of the fifteen candidate foraging models contain weak positive effects of ΔNDVI, suggesting that ibex spent more time foraging in areas of high NDVI relative to the study area average. However, this effect was not selected in the best foraging model.

Four SEMs – which link only the altitude and ΔNDVI sub-models – fit the data well according to Fisher's *C* statistic (Table 2). None of the SEMs linking all three sub-models (altitude, ΔNDVI and time spent foraging) fit the data adequately. We accepted model 1 in Table 2 as the best performing SEM (Fig. 2a). This model contains a strong positive effect of temperature on ibex altitude and a strong negative effect of altitude on ΔNDVI; these partial effects fit the data well (Fig. 2b-c). Additionally, this SEM contains a moderate negative effect of ibex age on altitude and a weak positive effect of ibex age on ΔNDVI (Fig. 2a). This latter effect indicates that older ibex used higher ΔNDVI areas, independent of the influence of altitude on ΔNDVI. The effect of aspect on ΔNDVI was also selected in the best SEM. The SEM results indicate that, when considering the hypothesized causal pathway as a whole, there is strong support for the pathway between temperature, altitude and ΔNDVI, but no strong evidence for an effect of ΔNDVI on time spent foraging. Put together, our results show that ibex traded off thermoregulation against time spent in areas of higher vegetation productivity, and did not compensate behaviorally for reduced vegetation productivity by adjusting time spent foraging.

There is some support for a negative effect of altitude on FCP: a negative effect of altitude is included in the two best FCP models (Table 3). This supports the SEM findings, indicating that reductions in vegetation productivity experienced due to upslope movements may also result in the consumption of lower quality forage (Fig. 5). However, the explanatory power of these models is relatively low (Table 3) and the null model was selected within the best FCP model set, indicating that the influence of altitude on forage quality is uncertain. There is a suggestion of higher FCP in older individuals, with a weak age effect being present in the best model.

Discussion

To date, the significance of trade-offs between thermoregulation and energy acquisition for species' responses to climate change has not been recognized. Our study provides strong evidence that male Alpine ibex trade off thermoregulation against foraging. Ibex moved to higher altitudes during the spring and summer, apparently to avoid high ambient temperatures. However, as a consequence, ibex moved to areas of lower NDVI relative to the study area average at that time. The protein content of ibex feces was lower in low NDVI areas, indicating that ibex consumed lower quality forage there. For temperate herbivore species, foraging conditions during the vegetation growing season exert a particularly strong influence on their fecundity and overwinter survival. As such, thermoregulation-foraging trade-offs could affect population dynamics as the climate warms.

Our study extends previous research on the role of daily variation in altitude-use for mountain ungulate thermoregulation (Aublet et al., 2009; Mason et al., 2014b), revealing that ambient temperature variation can drive seasonal altitudinal migration. As a result of altitudinal migration, ibex remained within a remarkably narrow ambient temperature range relative to the temperature fluctuations they would have experienced at a fixed altitude. This behavior will limit the need for autonomic thermoregulation, and consequently is likely to be an adaptation to reduce energetic expenditure and, potentially, to conserve water. However, as a result of upslope migration, ibex used areas of lower NDVI than if they had remained at lower altitudes. While NDVI has been widely used to represent forage productivity for mountain ungulates (Hamel et al., 2009; Mason et al., 2014a; Pettorelli et al., 2007), it can be affected by variation in the relative cover of bare rock, snow and vegetation in mountain environments (Elvidge and Lyon, 1985). As such, at high altitudes in our study area, where there is more bare rock and less vegetation, lower NDVI values are likely to indicate reductions in vegetation availability as well as quality. Similarly to a previous studies of mountain ungulates (Hamel et al., 2009), we found that NDVI correlated well with FCP (Fig. S2). This indicates that ibex foraging in higher NDVI areas consumed higher quality vegetation. So, while it is not possible here to disentangle the relative effects of vegetation quantity and quality on NDVI, NDVI does appear to be an appropriate proxy for forage quality. Additionally, there was some evidence for a negative effect of altitude on FCP, tentatively suggesting that ibex consumed lower quality vegetation as a consequence of moving to higher altitudes.

The trade-off we identified could have important implications for the energy budgets of alpine species. The snow-free period between May and October is critical for energy acquisition by mountain herbivores; outside this period, high-quality forage is scarce due to vegetation senescence and high snow cover during winter. As such, like other species inhabiting highly seasonal environments, ibex are unlikely to be able to compensate for reduced energy acquisition during spring and summer by foraging more during winter, so the trade-off identified here encompasses the main period during which ibex accumulate energy reserves for reproduction and survival. Our results indicate that ibex did not compensate behaviorally for reductions in forage availability or quality by adjusting their activity budgets during daylight hours, which were not influenced by ΔNDVI (see Tables 1c & 2). Ibex could adapt their foraging budgets in different ways. For instance, we found that ibex spent slightly more time foraging earlier in the morning of warmer days, which could compensate partially for reduced activity during the heat of such days (Fig. 4). However, our models indicate that increased foraging during the morning was followed by lower foraging activity in the afternoon and evening on warmer days, suggesting that any compensatory effect is weak. Another potential compensatory mechanism is increased nocturnal foraging during periods of hot weather, though low levels of night-time activity have been recorded in ibex during summer (Signer et al., 2011). Future work should be undertaken on the night-time behavior of this species in order to reveal whether ibex foraging activity is higher on nights following hotter days. Daily altitudinal movements – between lower altitudes in the morning and evening, and higher altitudes in the middle of the day – are another tactic that could buffer against the effects of seasonal altitudinal migration. However, in contrast to a previous study (Aublet et al., 2009), we did not detect a strong effect of this. While there was a suggestion that ibex moved firstly upslope and then downslope during the day (Table 1a), this effect was not selected in the best model and explained much less variation in ibex altitude than the pronounced effect of mean daily temperature.

The trade-off we identified is age-dependent: older individuals (i.e., larger ones) tended to use lower altitudes, as has been found previously (Aublet et al., 2009), and foraged in higher NDVI areas as a result. Additionally, a direct positive effect of age on ΔNDVI – independent of altitude-use – was selected in the best SEM. As a result of these effects, the energy acquisition of older individuals could be less impacted by high temperatures. There is weak evidence that older ibex had higher levels of FCP, but such an effect could reflect the tendency of larger ruminants to have higher endogenous protein concentrations in their feces (Van Soest, 1994) rather than the use of higher NDVI areas. The use of lower altitudes by older ibex could be due to age- and sizespecific variation in thermal tolerance or energetic requirements. For instance, larger ibex will warm up more slowly due to lower thermal conductance (Peters, 1986), so may exhibit delayed responses to increasing temperatures and use lower altitudes on average. Also, larger ibex have higher absolute but lower relative energetic requirements (Demment and Van Soest, 1985), which could influence their thermal tolerance or forage requirements. To investigate the drivers of the body size-altitude relationship would require detailed information on the effects of age and body size on temperature and energy budgets. The direct effect of age on ΔNDVI indicates that older individuals also used areas of higher productivity for a given altitude. This may indicate an influence of individual experience, social hierarchies (Bergeron et al. 2010) or energetic requirements on forage site selection.

The outcome of the thermoregulation-foraging trade-off varied across the season. Throughout most of the summer and autumn (July-October), ibex used areas with lower NDVI than the study area average. Indeed, the nadir in mean experienced NDVI actually coincided with peak study area NDVI. Only during spring (May-June), when ibex were using low altitude areas around 2,300 m, did they consistently experience higher NDVI than the study area average. Spring is a critical period for ungulates to acquire energy for growth, reproduction and survival (Gaillard et al., 1997; Langvatn et al., 1996), and spring conditions strongly influence ibex horn growth and survival (Giacometti *et al.* 2002; Pettorelli *et al.* 2007; Büntgen *et al.* 2014). Our results emphasize why spring conditions are so important for growth and vital rates in alpine ungulates. Ibex utilized areas of high vegetation productivity only during spring and early summer, before higher temperatures forced them to less productive areas. This could have important implications for ibex energy acquisition in the future. Our study indicates that it will be important to understand how mountain ungulates balance thermoregulation and foraging if springs become earlier and warmer in the future. While longer springs could be highly beneficial in terms of increased forage quality and availability, increases in spring temperature may reduce the duration for which animals can forage on abundant high quality vegetation at lower altitudes.

Our study adds an important new perspective to our understanding of the drivers of spatio-temporal variation in ungulate distributions. Previously, ungulates have been shown to select strongly for areas of high vegetation quality, due to the disproportionate benefits that increases in forage quality have on nutrient intake (Van Soest, 1994; White, 1983). We demonstrate that for male Alpine ibex during spring and summer, thermoregulation is an important driver of their distributions, appearing to override forage productivity in importance when temperatures are high. It had been suggested that ibex may benefit from upslope migration through delayed vegetation phenology at higher altitudes (Büntgen et al., 2014), as is the case for ungulates undergoing long migrations across latitudinal and altitudinal gradients (Albon and Langvatn, 1992; Hebblewhite et al., 2008). This was not the case in our study. It may be that variation in the timing of the snow-melt and consequent green-up across different altitudes was too small to generate a detectable altitudinal gradient in forage quality during the spring green-up. Indeed, a previous study in the same area reported negligible increases in forage quality with altitude early in the growing season (Aublet et al., 2009) compared to studies of ungulates in non-alpine environments (Albon and Langvatn, 1992). Further studies in different montane regions would help clarify the role of delayed vegetation phenology in altitudinal migration by mountain ungulates. More generally, our study demonstrates that research on the drivers of thermally sensitive prey distributions should consider not only trade-offs between predation risk and resources, but also between thermoregulation and these factors.

Here, we identified a trade-off in an alpine mammal, but trade-offs between thermoregulation and foraging could be a general phenomenon for thermally sensitive species (e.g., moose (*Alces alces*); Dussault *et al.* (2004)). Thermal specialists are predicted to have to expend more energy and water than thermal generalists to deal with climate change (Boyles et al., 2011). While behavioral thermoregulation may allow thermal specialists to reduce the costs of thermoregulation, our study shows that such behaviors can restrict animals from profitable areas for resource acquisition, which could affect survival and reproduction negatively in the future. While here we have focused on males, future studies on thermoregulation-foraging trade-offs in females, which contribute most to the population dynamics of many animal species, would be valuable. Investigating such trade-offs could greatly improve our understanding of how animal populations will respond to climate change. Models such as ours, based on relationships between environmental temperature and behavior or distribution, can provide key insights into the drivers of thermoregulation-foraging trade-offs. However, to predict how trade-offs will affect future population responses requires information on the effects of fine-scale temperature variation on behavior and energy budgets. Optimal annual routine modeling is a technique that is ideally suited to this as it allows the relationships between behavior, energetics and life-histories to be quantified (McNamara and Houston, 2008). Such models could be parameterized using field data on behavior and energetics, both of which can now be inferred indirectly using tri-axial accelerometry (Gleiss et al., 2011). Future work using these techniques could provide invaluable insights into the predicted impacts of climate change on the population dynamics of thermally sensitive species.

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Data Accessibility

The data used in this study are available on Dryad (Mason et al., 2017).

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Tables

Table 1. Candidate SEM sub-models of ibex altitude (a), ΔNDVI (b) and time spent foraging (c). Models considered are within 6 ΔAIC of top models. Standardized coefficients, log-likelihood (LL), number of parameters (*K*), difference in AIC with top model (ΔAIC) and marginal R^2 (i.e., for fixed effects only) are displayed for each model. All models were fitted with individual-level random intercepts. Null models are displayed for comparison. In a) and c), time was considered as a quadratic effect only (Time + Time^2).

a) Altitude

Age	Temp	Time	Time^2	*K*	LL	ΔAIC	R^2
-0.20	0.47			5	-473.39	0.00	0.25
-0.19	0.47	0.23	-0.29	7	-472.36	1.94	0.26
				3	-523.17	95.56	

b) ΔNDVI

Age	Altitude	Aspect	Slope	*K*	LL	ΔAIC	R^2
	-0.65	0.14		5	-424.36	0.00	0.44
0.06	-0.64	0.13		6	-423.43	0.15	0.44
	-0.65	0.13	-0.03	6	-424.04	1.37	0.44
0.06	-0.64	0.12	-0.04	7	-423.05	1.38	0.44
				3	-530.08	207.46	

c) Time spent foraging

Age	Aspect	ΔNDVI	Slope	Temp	Time	Time^2	Time:Temp	*K*	LL	ΔAIC	R^2
				-0.11	-5.97	5.89	-0.19	7	-422.08	0.00	0.44
		0.05		-0.09	-5.95	5.87	-0.18	8	-421.21	0.27	0.44
-0.05		0.06		-0.09	-5.97	5.89	-0.18	9	-420.30	0.45	0.44
-0.04				-0.11	-5.99	5.91	-0.19	8	-421.50	0.84	0.44
	0.03			-0.11	-5.93	5.86	-0.19	8	-421.77	1.39	0.44
			-0.02	-0.11	-5.97	5.89	-0.19	8	-421.98	1.81	0.44
	0.02	0.05		-0.10	-5.92	5.85	-0.18	9	-421.03	1.91	0.44
-0.05	0.02	0.06		-0.09	-5.94	5.87	-0.18	10	-420.14	2.12	0.45
		0.05	-0.01	-0.10	-5.95	5.87	-0.18	9	-421.15	2.15	0.44
-0.04	0.03			-0.11	-5.95	5.87	-0.19	9	-421.18	2.21	0.44

-0.05		0.06	-0.01	-0.09	-5.97	5.89	-0.18	10	-420.26	2.37	0.45
-0.04			-0.02	-0.11	-5.99	5.91	-0.19	9	-421.42	2.69	0.44
	0.03		-0.01	-0.11	-5.94	5.86	-0.19	9	-421.74	3.32	0.44
	0.02	0.05	-0.01	-0.10	-5.93	5.85	-0.18	10	-421.01	3.86	0.44
-0.05	0.02	0.06	-0.01	-0.10	-5.94	5.87	-0.18	11	-420.12	4.10	0.45
-0.04	0.03		-0.01	-0.11	-5.95	5.88	-0.19	10	-421.16	4.16	0.44
								3	-530.18	208.21	

Table 2. Best performing SEMs of ibex altitude and ΔNDVI. All models performing adequately according to directional separation tests (i.e., $P > 0.05$) are shown. Marginal R^2 (i.e., for fixed effects only) of sub-models, Fisher's C statistic with associated degrees of freedom and P-value, number of parameters (K) and difference in AIC with top model (ΔAIC) are displayed. AIC were calculated with Shipley's (2013) method for SEMs. Models selected according to the model nesting rules of Richards (2008) are indicated with tick marks.

Model	**1**	**2**	**3**	**4**
Altitude ~ Temperature	x	x	x	x
Altitude ~ Age	x	x	x	x
ΔNDVI ~ Altitude	x	x	x	x
ΔNDVI ~ Aspect	x	x	x	x
ΔNDVI ~ Age	x		x	
ΔNDVI ~ Slope			x	x
Altitude R^2	0.25	0.25	0.25	0.25
ΔNDVI R^2	0.44	0.44	0.44	0.44
Fisher's C	6.13	10.21	8.08	12.35
df	4	6	6	8
P-value	0.19	0.12	0.23	0.14
K	11	10	12	11
ΔAIC	0.00	2.08	3.95	6.22
Selected	✓	✓		

Table 3. Best performing models of ibex fecal crude protein content. Standardized coefficients ± SE, log-likelihood (LL), number of parameters (*K*), difference in AICc with top model (Δ AICc) and marginal R^2 (i.e., for fixed effects only) are displayed for each model. All models were fitted with individual and day of year random intercepts. The null model is displayed for comparison.

Age	Altitude	*K*	LL	ΔAICc	R^2
0.58 ± 0.29	-1.05 ± 0.40	6	-157.84	0.00	0.13
	-1.06 ± 0.41	5	-159.79	1.50	0.09
0.58 ± 0.29		5	-160.72	3.34	0.02
		4	-162.62	4.82	

Figures

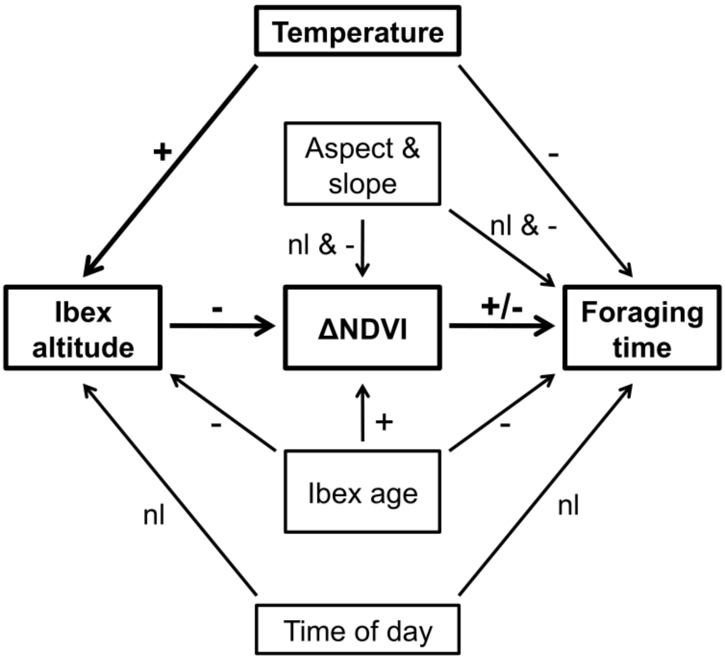

Figure 1. Path diagram of the hypothesized maximal structural equation model of ibex altitude, ΔNDVI and foraging time. ΔNDVI is the difference between the NDVI of an ibex location and the mean NDVI of the study area at that time. Arrows indicate hypothesized causal pathways between predictors and response variables. The direction of hypothesized effects is provided, with ‘+’, ‘-’ and ‘nl’ indicating positive, negative and non-linear effects, respectively. The main pathway of interest is shown in bold.

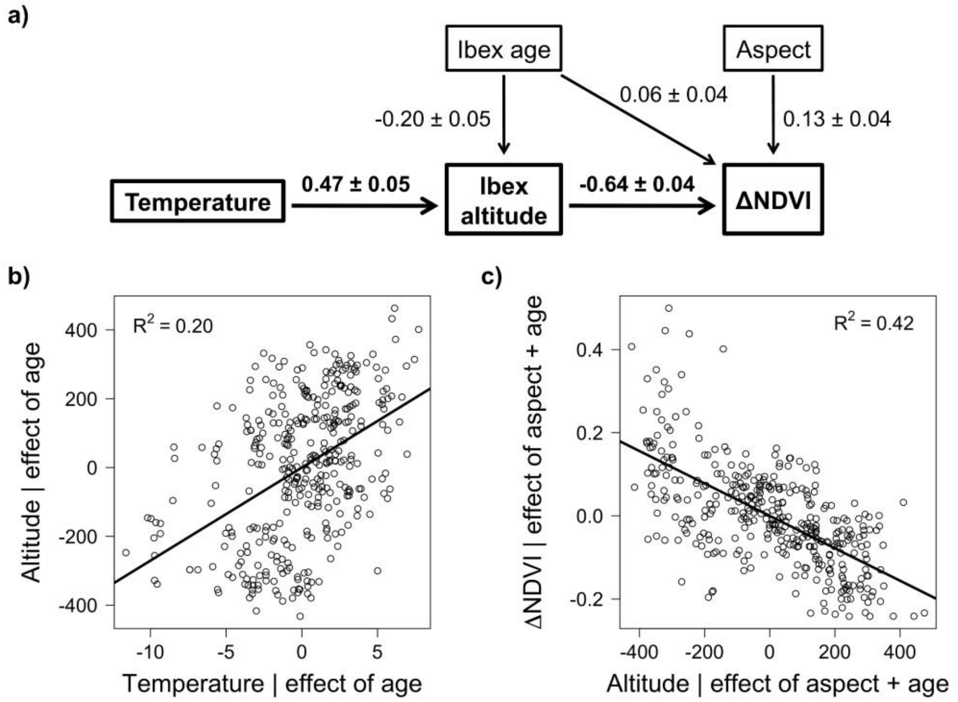

Figure 2. Path diagram of the best fitting structural equation model of ibex altitude and ΔNDVI (a) and partial effects plots showing the two main effects of interest (b-c). In a), arrows indicate hypothesized causal pathways between predictors and response variables. The main causal pathway of interest is shown in bold. Path coefficients ± SE are displayed. Panel b) shows the partial effect of mean daily temperature (recorded by the study area's weather station) on ibex altitude, where 'temperature| effect of age' and 'altitude| effect of age' are variation in temperature and altitude, respectively, while statistically controlling for the effect of age. Panel c) shows the partial effect of ibex altitude on ΔNDVI (the difference between ibex location NDVI and mean study area NDVI), where 'altitude| effect of aspect + age' and 'ΔNDVI| effect of aspect + age' are variation in altitude and ΔNDVI, respectively, while statistically controlling for the effects of aspect and age. Adjusted R^2 values are displayed for partial effects.

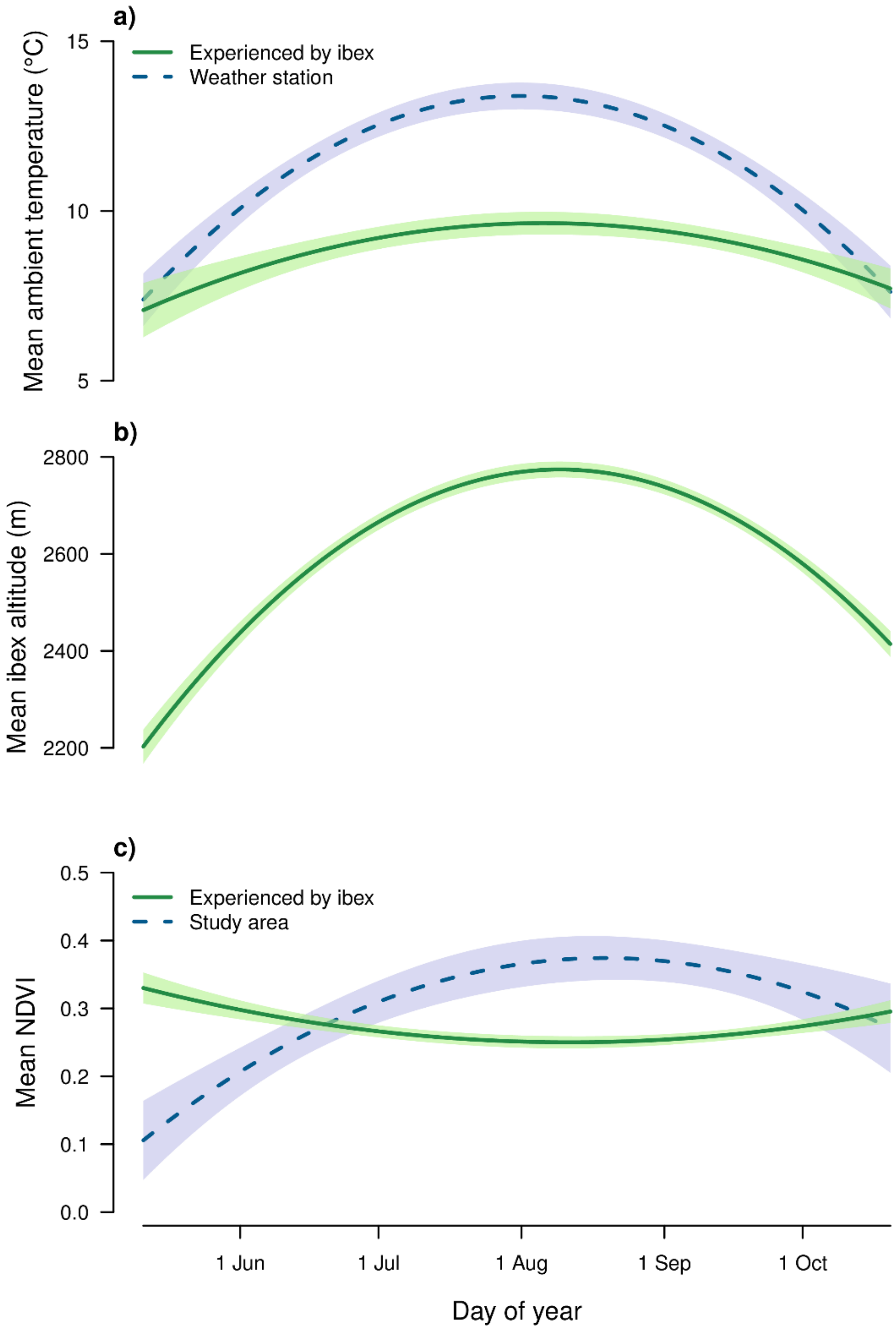

Figure 3. Seasonal variation in ambient temperature (a), altitude (b) and NDVI (c) experienced by 43 male Alpine ibex between May and October 2011. Solid lines are best fits for seasonal trends in conditions experienced by ibex and shaded areas are fits ± standard error. In a), the dashed line is the best fit for the trend in mean temperature during daylight hours from the study area's weather station (at 1,951m). Temperature

experienced by ibex was recorded by iButton data-loggers at the locations of observations. In c), the dashed line is the best fit for the trend in mean study area NDVI.

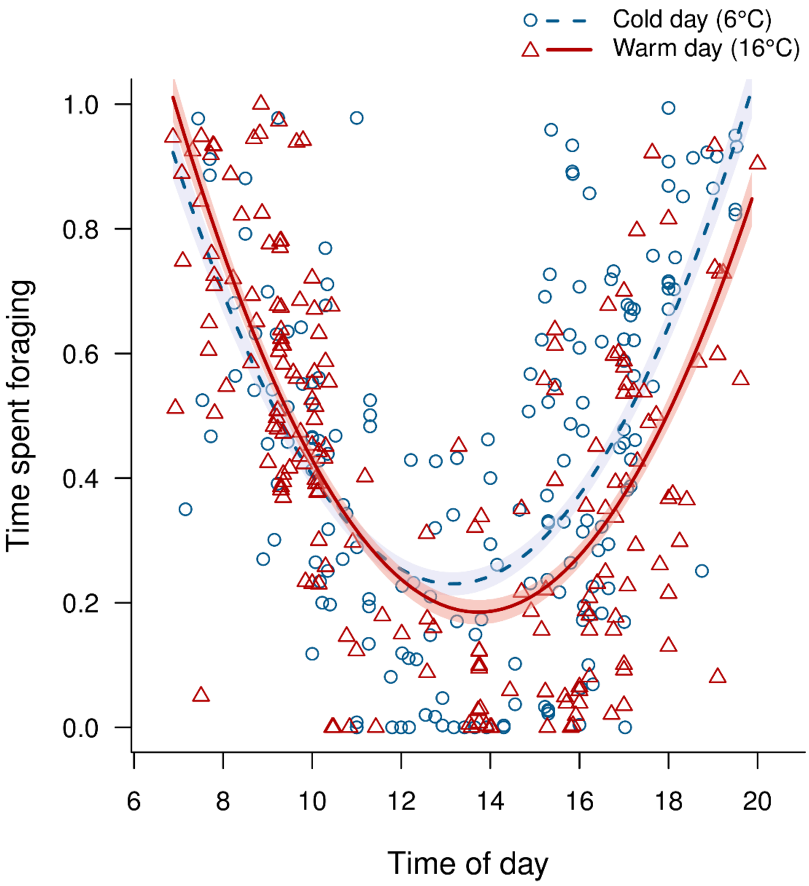

Figure 4. The interactive effects of time of day and mean daily temperature on time spent foraging by ibex. Fitted lines are population-level predictions ± SE from the top foraging time model (see Table 1c) of the effect of time of day on time spent foraging on typical cold (6°C; dashed) and warm (16°C; solid) days. Circles and triangles are observations from colder (0-12°C) and warmer (13-20°C) days, respectively.

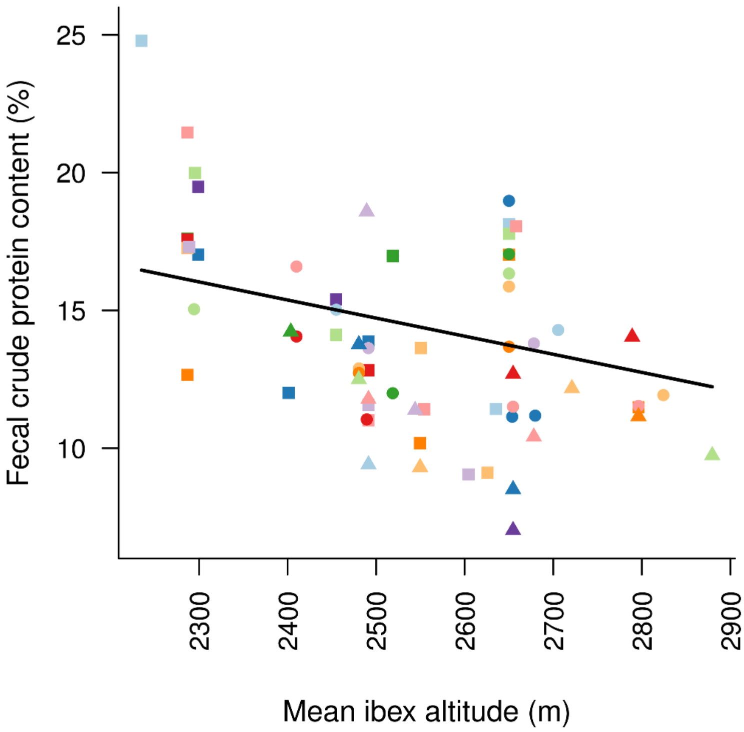

Figure 5. The relationship between ibex altitude-use and fecal crude protein content. Each unique color-symbol combination represents a different individual. The fitted line is the population-level prediction from the top fecal crude protein model, with age set to its mean value.