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Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects

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Abstract

The altitudinal shifts of many montane populations are lagging behind climate change. Understanding habitual, daily behavioural rhythms, and their climatic and environmental influences, could shed light on the constraints on long-term upslope range-shifts. In addition, behavioural rhythms can be affected by interspecific interactions, which can ameliorate or exacerbate climate-driven effects on ecology. Here, we investigate the relative influences of ambient temperature and an interaction with domestic sheep (*Ovis aries*) on the altitude use and activity budgets of a mountain ungulate, the Alpine chamois (*Rupicapra rupicapra*). Chamois moved upslope when it was hotter but this effect was modest compared to that of the presence of sheep, to which they reacted by moving 89–103 m upslope, into an entirely novel altitudinal range. Across the European Alps, a range-shift of this magnitude corresponds to a 46% decrease in the availability of suitable foraging habitat. This highlights the importance of understanding how factors such as competition and disturbance shape a given species' realised niche when predicting potential future responses to change. Furthermore, it exposes the potential for manipulations of species interactions to ameliorate the impacts of climate change, in this case by the careful management of livestock. Such manipulations could be particularly appropriate for species where competition or disturbance already strongly restricts their available niche. Our results also reveal the potential role of behavioural flexibility in responses to climate change. Chamois reduced their activity when it was warmer, which could explain their modest altitudinal migrations. Considering this behavioural flexibility, our model predicts a small 15–30 m upslope shift by 2100 in response to climate change, less than 4% of the altitudinal shift that would be predicted using a traditional species distribution model-type approach (SDM), which assumes that species' behaviour remains unchanged as climate changes. Behavioural modifications could strongly affect how species respond to a changing climate.

Keywords: activity budget, altitudinal migration, behaviour, behavioural thermoregulation, chamois, climate change, interspecific interactions, range-shift, temperature, ungulate

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Introduction

Mountainous regions contain a high proportion of the world's biodiversity (Lomolino, 2001; Orme *et al.*, 2005), including a range of species with unique adaptations and high extinction risk (Jetz *et al.*, 2004; Ricketts *et al.*, 2005). Montane species are particularly vulnerable to climate change (e.g., Bohm *et al.*, 2001). Long-term upslope range-shifts driven by temperature increases have been recorded in many montane species but, in numerous cases, range-shifts are lagging behind climate change (Chen *et al.*, 2011). Our understanding of long-term altitudinal range-shifts of species and, in particular, the constraints on upslope range changes, could be improved by considering how populations habitually respond to environmental cues over shorter time periods. In mountainous environments, species undergo altitudinal migration both seasonally and diurnally in response to climatic and environmental variation (Geist, 1971; Aublet *et al.*, 2009; Boyle *et al.*, 2010). Models linking such behavioural routines to climate are uncommon (but see Dunbar, 1998; Korstjens *et al.*, 2010; Melin *et al.*, 2014) and tend to focus on single species, failing to account for the interspecific interactions that can explain the absence of species from large portions of their fundamental niche (Connell, 1961; Silander & Antonovics, 1982; Huntley *et al.*, 2004). Studies of diurnal migratory rhythms, considering multiple competitors, would reveal the relative roles of climate and of biotic interactions in controlling altitudinal range. This could shed light on the potential for species to track climate change in mountainous regions.

Many animals exhibit diurnal behavioural rhythms strongly entrained to variation in environmental cues,

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such as light intensity and temperature. Such rhythms are important in controlling the energy balance of a species (Aschoff, 1979). In endotherms, temperature can exert a particularly strong influence over the timing of, and allocation of energy reserves to, vital behaviours such as foraging, resting, and moving between habitat patches (Dunbar, 1992; Korstjens *et al*., 2010). Adjusting behaviour in response to ambient temperature is generally thought to be less energetically expensive than autonomic thermoregulation (Dussault *et al*., 2004; Maloney *et al*., 2005). Behavioural thermoregulation can entail moving to cooler areas such as higher altitudes (Aublet *et al*., 2009) or microclimates (Melin *et al*., 2014; Scheffers *et al*., 2014), reducing activity during the hottest parts of the day (Aublet *et al*., 2009) or actively performing heat-dissipation behaviours, such as wing spreading in birds (Du Plessis *et al*., 2012) and saliva spreading in marsupials (Needham *et al*., 1974). In ectotherms, the potential for behavioural thermoregulation to buffer the impacts of climate change has already been noted (Kearney *et al*., 2009) and the same could be true for endotherms. Many species can simultaneously adjust multiple behaviours (e.g., Ricklefs & Hainsworth, 1968; Dawson *et al*., 2006; Chapperon & Seuront, 2011), increasing the complexity of potential behavioural responses to climate change. For example, mobile montane species, can both move upslope and reduce their activity when it is hotter (Aublet *et al*., 2009). An ability to survive across a wide climatic range by adjusting activity budgets could reduce the need for certain species to move to higher elevations, possibly making them more adaptable to climate change.

Behavioural routines are also strongly influenced by a range of nonclimatic factors, including the availability of resources (e.g. Lehmann *et al*., 2008), population density (e.g. Mobaek *et al*., 2008), and interactions with other species (e.g. Wauters *et al*., 2001). Interspecific interactions, in particular, also exert an important influence on range-shifts under climate change (Araujo & Luoto, 2007; Suttle *et al*., 2007; Van Der Putten *et al*., 2010). For tightly linked species, such as insects and their host plants, the effect of biotic interactions can be stronger than climate effects on range extent, even at a continental scale (Araujo & Luoto, 2007). However, to date, the role of less specialised interactions, for example interference or exploitation competition between different species, has been overlooked. Interspecific interactions may prove particularly important in mountainous environments, as climate change pushes populations upslope into an ever diminishing area of habitat (Chen *et al*., 2011), potentially bringing different species into competition. For instance, in guilds of mountain ungulates, where there is often a high degree of dietary overlap among species (Bertolino *et al*., 2009), upslope migration due to climate change could increase range overlap and competition for resources, particularly if species respond individualistically to change (e.g. Mair *et al*., 2012). Competitive exclusions among mountain ungulate species are thought to have caused local extinctions in the past (Mishra *et al*., 2006). Understanding the influence of interspecific interactions on daily patterns of altitude use could greatly improve future projections of range-shifts in mountainous areas, particularly at small spatial scales.

Predicting how behaviours will be altered in the future is difficult because long-term behavioural adaptation to climatic and environmental change, through phenotypic plasticity (Przybylo *et al*., 2001) or microevolution (Reale *et al*., 2003), might not be predictable from current conditions. Ultimately, to predict how populations adapt to a changing climate requires long-term observational data (e.g. Clutton-Brock & Pemberton, 2004) or experimental studies (e.g. Ayrinhac *et al*., 2004). However, for most populations, long-term behavioural data are not available and, for many, experimentation is not feasible. In such cases, studies of the current relationship between behaviour and climate can shed light on the plasticity of a species' behavioural response to climatic variation (Dunbar, 1998; Lehmann *et al*., 2008; Korstjens *et al*., 2010). Such approaches could be used to infer whether behavioural plasticity alone is sufficient for populations to remain in equilibrium with climate, as has been done for phenological plasticity using current relationships between phenology and climate (Phillimore *et al*., 2010). Studies conducted over short time-scales could identify whether a different mechanism of long-term adaptation, such as microevolution, will be required for populations to keep track with climate change.

Here, we use a natural experiment to study the effects of temperature and interspecific interactions on the diurnal behaviour of Alpine chamois (*Rupicapra rupicapra*) during the summer in a high mountain environment. Chamois are relatively eurythermic, adapted to a wide range of temperatures, and are found across a broad altitudinal range in the Alps (500–3100 m) (Shackleton, 1997; Spitzenberger *et al*., 2001). We focus on a high altitude population, occurring between approximately 2450 and 2800 m during summer. We evaluate the roles of two behaviours in thermoregulation: altitudinal migration and adjustments to activity budgets. We concentrate on adult females as they generally dictate habitat selection in chamois groups (Knaus & Schröder, 1983) and females exert the greatest influence on ungulate population dynamics (Gaillard *et al*., 2000). Mountain ungulates typically show pronounced behavioural thermoregulation, migrating to higher altitudes in the heat of the day when it is warmer and *vice versa* (Aublet *et al*., 2009). They also devote more time to resting and rumination, and less time to foraging, during the hottest part of the day (Green & Bear, 1990; Shi *et al*., 2003). When temperatures get too high, these rhythms can be interrupted altogether: in chamois, normal feeding behaviour ceases at temperatures above 28 °C (Hamr & Czakert, 1986). Chamois behaviour can also be affected by other ungulate species; for example, introduced mouflon (*Ovis orientalis musimon*) are thought to have displaced chamois in some areas of the Pyrenees (Gonzalez, 1987). Furthermore, Alpine chamois actively avoid other ungulate species, moving to sheltered areas when mouflon or domestic sheep (*Ovis aries*) are present (Chirichella *et al*., 2013). Here, we take advantage of the annual introduction of sheep to the study area during summer to investigate the influence of this species on chamois behaviour. Behavioural observations were undertaken in the presence and absence of sheep, allowing us to examine the effects of interspecific competition and temperature. Structural equation modelling (SEM) was used to investigate the interplay between temperature, interspecific interactions, altitude use, and time spent foraging. Using these relationships, we make inferences about the potential influences of climate change and interspecific interactions on chamois behaviour.

Materials and methods

Data collection

The study area is Lauson, located in Cogne valley, Gran Paradiso National Park, Italy (GPNP; 45°34′ N, 7°18′ E) (Fig. 1). The area contains approximately 200 Alpine chamois. Chamois in GPNP are protected from hunting and have very few natural predators. The summer altitudinal range of chamois here is between 1600 m and 3100 m above sea level, with groups of females and kids generally occurring from 2500 m upwards. Above the tree-line (at approximately 2200 m), the area is characterised by alpine meadows, grassland with scattered rocks, open rock faces, moraines, and scree slopes. Above 2880 m, vegetated habitat is replaced by bare rock and permanent snow and ice. The maximum elevation is 3314 m.

A population of unmarked individuals (mean group size, 21.6 ± 0.3), predominantly females and kids, was monitored between June and July 2012. The study was conducted over this period to coincide with the introduction of sheep into the area, which occurred approximately halfway through the study period. On the 12th July, circa 100 domestic sheep, intermittently associated with shepherds and sheep-dogs, were introduced to the lower altitudes of the valley (approximately 2250–2400 m) and remained there throughout the remainder of the study period. This created two treatment periods over which to investigate the effect of interspecific interactions: sheep absent (13 days) and sheep present (14 days). The study was restricted to this short period to reduce the potential confounding effects of seasonal variation in behaviour, climate, and resource availability between the two treatments. Alpine ibex (*Capra ibex*), another potential competitor of chamois, are also found in the area. However, ibex are generally restricted to higher altitude areas of the Cogne valley during summer and were rarely observed in Lauson during the study period.

Chamois were observed between 6:10 hours and 20:30 hours daily using binoculars and a spotting scope. At 5 min intervals, the mean altitude of a group's location was derived from a 1 : 25 000 scale map of the study area (hereafter 'altitude use'). Instantaneous scan samples (Altmann, 1974) were performed and the activities of all visible individuals were recorded. Activities were classified as resting, standing, moving, foraging, and 'other' (drinking, salt-licking, urinating and defecating). In total, 914 scans were performed, distributed evenly throughout the study period. All scan sampling sessions lasted for a minimum of 1 h. The timing of sampling sessions varied from day to day, depending on visibility and

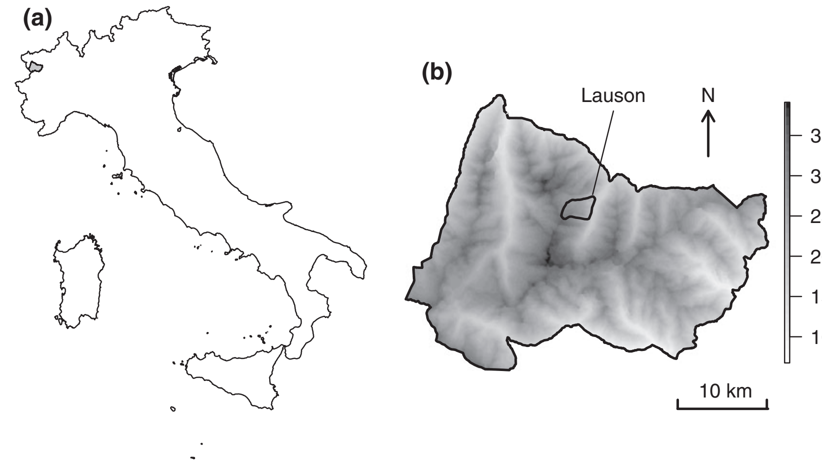

Fig. 1 Map of (a) Italy, displaying the location of Gran Paradiso National Park (GPNP) in grey, and (b) GPNP, indicating the location of the study area, Lauson. Shading indicates altitude in metres.

the time taken to locate chamois between sampling sessions. At each time interval, the local air temperature ($temp_{local}$) was recorded using two Gemini TinyTalk TK-0014 data-loggers placed at the same elevation as the group (at the observer's location). One of these was wrapped in foil and placed in the shade, to reduce the effect of direct solar radiation (hereafter 'screened temperature') and one was exposed to direct solar radiation (hereafter 'unscreened temperature'). These different temperature measures were recorded to provide insight into the relative roles of ambient temperature and solar radiation in thermoregulation. Both air temperature and solar radiation are thought to play a role in mammalian heat exchange (Porter *et al*., 2000) but their relative importance is likely to vary among species and environments. We also recorded screened temperature data from a fixed altitude location in our study area at 2600 m ($temp_{fixed}$), which we could relate to daily variation in chamois altitude use, without being confounded by decreasing ambient temperature with increasing altitude. We were not able to record unscreened temperature data from a fixed altitude, so unfortunately we did not examine the influence of solar radiation on altitude use.

Statistical analysis

We applied SEMs, using the 'lavaan' package in R (Rosseel, 2012), to model the interplay between altitude use, foraging, temperature, time of day, and the presence of sheep. SEM is a multivariate modelling approach that allows for collinearity among predictors. We fitted models to examine the effects of seven predictor variables – time of day, time of day^2, presence of sheep, $temp_{fixed}$, $temp_{local}$, altitude use, and group size – on three response variables: altitude use, local temperature, and foraging (see Fig. 2). Group size was the number of adult females in a group at a given time and was used to test for the presence of density dependence in time spent foraging. Time of day was converted to minutes and so varied between 370 (6:10 hours) and 1230 (20:30 hours). Based on our *a priori* expectations, we allowed quadratic effects of time of day on all three response variables. We also considered a quadratic effect of $temp_{local}$ on foraging. All other predictors had linear effects. The two response variables of principal interest are altitude use and foraging. Altitude use is continuous, and was modelled using a gaussian error structure. Foraging is binary (within each scan sample individuals were classified as 1 if foraging and 0 for any other behaviour) and was modelled using a binomial error structure. Model predictions of foraging were expressed as the probability that individuals are foraging in a given set of environmental conditions, which logically equates to the proportion of time spent foraging by chamois. Hereafter, this is referred to as 'time spent foraging'.

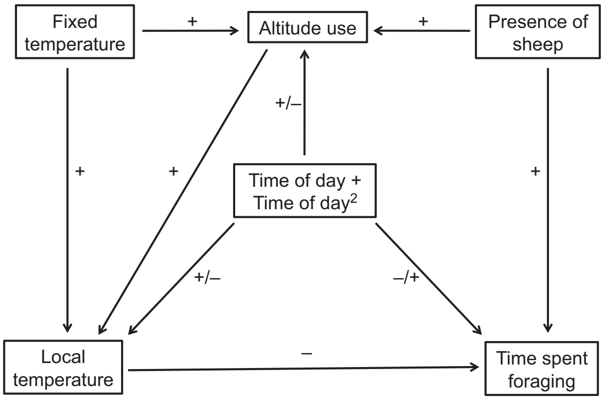

Fig. 2 Path diagram showing the variables and effects present in the most parsimonious structural equation model (i.e. that with the lowest Akaike Information Criterion) of chamois altitude use and time spent foraging. Arrows indicate hypothesised causal pathways, from predictors to response variables. Directions of effects are shown.

We fitted 28 models with ecologically sensible combinations of predictors, which were selected based on ecological theory and preliminary data exploration (see Table S1). We fitted models using either screened or unscreened temperature as the $temp_{local}$ variable, giving 56 models in total. The most complex model considered included 15 effects of predictors, across the three response variables. To assess model performance we used the chi–squared test and the root mean square of error approximation (RMSEA), both of which are commonly used goodness-of-fit tests for assessing SEMs (Chen *et al*., 2008). In SEM, model fit is determined by comparing the observed variable covariance matrix to the modelled covariance matrix. We considered as acceptable, models with nonsignificant chi-square and RMSEA *P*-values, i.e. where the observed and modelled covariance matrices did not differ significantly. From the set of acceptable models, we identified the most parsimonious using the Akaike Information Criterion (AIC), considering models with a ΔAIC of $\leq$6 and lower than the ΔAIC of all simpler nested models as having some support (Richards, 2008). Using the most parsimonious model, we modelled how the altitude use and the proportion of time spent foraging by chamois varied across a range of different times of day, different temperatures and with and without sheep.

To demonstrate how climate change could affect altitude use, we simulated future temperature change by increasing our fixed-altitude temperature observations ($temp_{fixed}$) by 5 °C, the most extreme mean temperature increase during summer predicted for the region by 2100 (IPCC, 2007). For all other predictors, we used the data observed during the study. We made predictions of future altitude use using our most parsimonious model (Table 1). Using these predictions, we defined the altitudinal ranges used by chamois during summer in four different scenarios: present day, sheep either absent or present; and 2100, sheep either absent or present. Altitudinal ranges were defined by the upper and lower bounds of confidence intervals of predicted altitude use, across all times of day. Next, from the altitudinal range use predicted by our most parsimonious model, we calculated the area of available foraging habitat in each scenario. We made our predictions across the entire spatial range of the species, which encompasses the whole of the European Alps (Shackleton, 1997). At present, there are no fine-scale predictions of changes to the distribution or productivity of forage vegetation as a result of climate change; consequently, our predictions assume that land-cover remains unchanged in 2100. We estimated available foraging habitat using the Corine land-cover 2006 data set at 100 m resolution (EEA, 2010) and digital elevation data at 90 m resolution from the Shuttle Radar Topography Mission (Jarvis *et al*., 2008). For the altitudinal ranges predicted by our model, the predominant Corine land-cover classes present are bare rock, glaciers/perpetual snow, natural grassland, and sparsely vegetated areas. Potential foraging habitat was defined as the area covered by either natural grassland or sparse vegetation. Ground-truthing in the study area confirmed that chamois foraged predominantly in these areas. To compare the potential change in altitude use and time spent foraging resulting from climate change and sheep presence, predictions were made across all times of day using mean values for all other predictors (as in Fig. 4 for altitude use). The upper and lower 95% confidence intervals (Efron & Tibshirani, 1991) of these predictions were used to calculate mean potential change in altitude use and time spent foraging from these predictions, accounting for uncertainty.

Results

Two SEMs fitted the observed data well, having both nonsignificant chi–squared and RMSEA *P*-values, and were thus deemed acceptable (see Table S2). Of these, one SEM was more parsimonious, having a lower AIC, and containing fewer parameters (Table 1, Fig. 2). Since there were no simpler nested or other competing models within 6 ΔAIC of this model, we had confidence that it was the best performing model. The best model performs well in predicting variation in mean altitude use (Fig. 3a, b) and mean time spent foraging (Fig. 3c, d), both with time of day and temperature. There is one case when the model does not deal perfectly with collinearity; the model predicts a positive, albeit weak, effect of altitude use on local temperature (Table 1). In fact, this relationship is probably due to the tendency of chamois to use high altitudes when it was warmer.

Table 1 Standardised effect sizes of each predictor (first column) in the most parsimonious structural equation model (i.e. that with the lowest Akaike Information Criterion). The response variables (first row) are altitude use of chamois (Altitude), the temperature recorded at location of chamois group ($\text{Temp}_{\text{local}}$), and time spent foraging by chamois (Foraging). The predictors are time of day (Time), time of day^2 (Time^2), presence of sheep (Sheep), temperature recorded from a fixed altitude ($\text{Temp}_{\text{fixed}}$), $\text{Temp}_{\text{local}}$, $\text{Temp}_{\text{local}}{}^2$, Altitude, and group size (Group). K indicates the number of parameters in the model, which is composed of 12 regression coefficients, intercepts for each variable (seven), variance parameters for each variable (seven), and six covariance parameters between different variables. The chi-square test statistic, root mean square of approximation (RMSEA) ± 95% confidence intervals, and *P*-values for each metric are shown. Nonsignificant *P*-values (>0.05) for these metrics indicate a well-fitting model

	Altitude	$\text{Temp}_{\text{local}}$	Foraging
Time	1.98	2.60	−0.82
Time^2	−1.86	−2.76	0.84
Sheep	0.62		0.07
$\text{Temp}_{\text{fixed}}$	0.23	0.39	
$\text{Temp}_{\text{local}}$			−0.14
$\text{Temp}_{\text{local}}{}^2$			
Altitude		0.09	
Group			
Chi–square	1.55		
P-value	0.67		
RMSEA	0.000 (0.000–0.012)		
P-value	1.00		
K	32		

We found strong evidence for a quadratic effect of time of day on chamois altitude use and foraging (Table 1, Fig. 3a, c). Chamois showed a strong diurnal pattern of altitudinal variation, moving from lower altitudes in the morning to high altitudes in the middle of the day before descending to lower altitudes again in the evening (Fig. 3a). While our data suggest that chamois remain at higher altitudes in the evening when sheep are present, there was no evidence to support this from model selection: the relationship between altitude use and time differed only in the intercepts for the two treatments (Fig. 3a). Chamois also exhibited diurnal rhythms in their activity budgets, spending most time foraging at dawn and dusk, and the least time foraging in the middle of the day (Fig. 3c). We also found strong evidence for an effect of temperature, independent of time of day, on both altitude use, and time spent foraging (Table 1, Fig. 3b, d). At higher temperatures, chamois moved upslope 8–11 m per 1 °C increase in screened temperature (Fig. 3b) and spent 0.8–1% less time foraging per 1 °C increase in unscreened temperature (Fig. 3d). Unscreened temperature was selected as the $\text{temp}_{\text{local}}$ variable in the most parsimonious model and, thus, is better supported as a predictor of time spent foraging than screened temperature. This suggests that chamois activity budgets are affected by solar radiation, rather than simply air temperature. We found no evidence for an effect of group size on activity budgets, suggesting an absence of pronounced density dependence (Table 1).

The presence of sheep had a very strong effect on altitude use. When sheep were present, the mean altitudinal range used by chamois was shifted strongly upwards, with chamois migrating on average a further 89–103 m upslope, according to our model (Fig. 3 a, b; Fig. 4a). This shift entailed moving from lower altitude areas of alpine meadow to more sparsely vegetated areas. Across the European Alps, this upward shift would result in a 46% decrease in the area of suitable summer foraging habitat for high altitude chamois

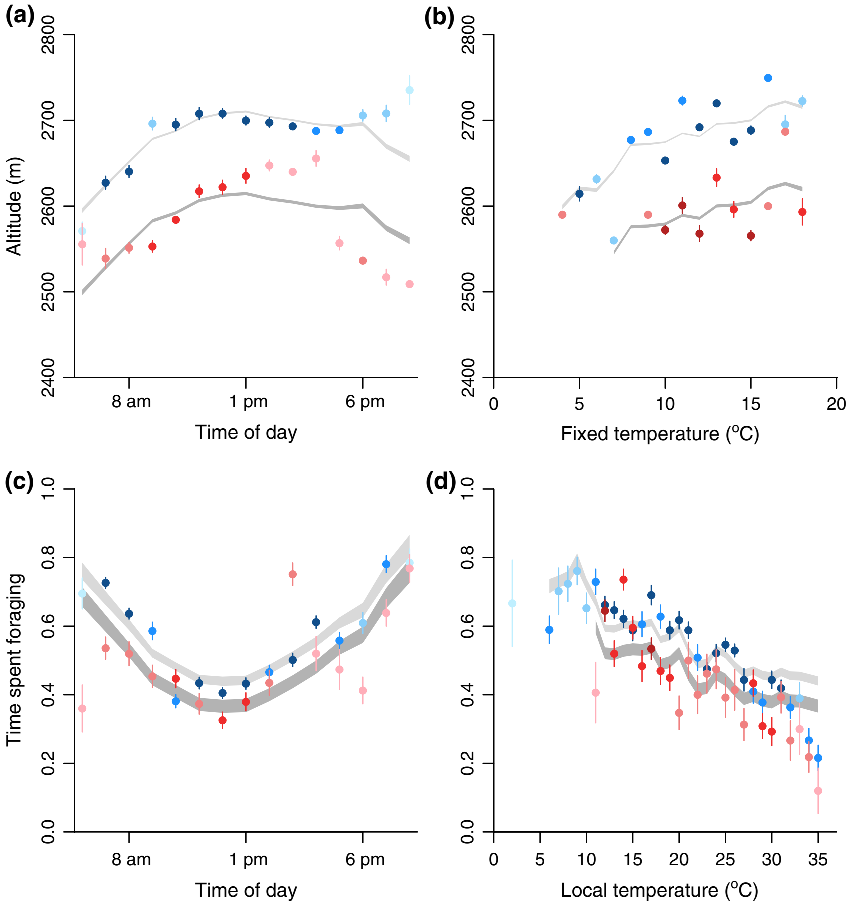

Fig. 3 Variation in observed (points) and predicted (shaded areas) chamois altitude use (a–b) and time spent foraging (c–d). Observed data are mean values calculated across all scan samples within hourly or one-degree temperature bands, and are weighted by the number of individuals recorded per scan sample. Means were calculated separately for when sheep were present (blue points) and absent (red points). Darker coloured symbols indicate observed means calculated from a higher number of scan samples and thus data with a higher weight in our analysis. Lines show standard errors of observed data. Predicted data are 95% confidence intervals of the weighted mean predicted values, for each hourly or one-degree band, from the most parsimonious structural equation model (i.e. that with the lowest Akaike Information Criterion) fitted to 1000 bootstrapped replicates (Efron & Tibshirani, 1991). Light and dark grey areas represent predicted values for sheep-present and sheep-absent scenarios, respectively.

populations. It should be noted that the mean fixed altitude temperature was marginally higher in the sheep-present period than the sheep-absent period (mean $\text{temp}_{\text{fixed}}$ ± standard error: sheep absent, 9.04 °C ± 0.25; sheep present, 9.94 °C ± 0.21). However, our results highlight that sheep presence, not temperature change was responsible for the observed upslope altitudinal shift: sheep had a much stronger effect than fixed temperature on altitude use and no models without an effect of sheep on altitude use fitted the observed data adequately (Table S2). Extrapolating from the response of chamois to diurnal temperature variations suggests that the potential effect of increasing temperature (due to climate change) on altitudinal range is likely to be weaker than the effect of sheep presence. For example, by this method a future 5 °C temperature increase is forecast to move the altitudinal range 15–30 m upslope on average (Fig. 4a), resulting in a 12% decrease in the available area of foraging habitat. If both the interaction with sheep and climate change affected chamois in the future, their altitudinal range would move 112–125 m upslope, reducing foraging habitat by 55%. Using the same approach, a future 5 °C temperature increase is forecast to reduce the daily proportion of time spent foraging by a maximum of 10%. The presence of sheep only influenced weakly the time chamois spent foraging, with chamois foraging on average for 2–13% longer in their presence (Fig. 3c, d).

Discussion

Diurnal altitudinal migration in chamois was influenced by temperature; however, this effect was dwarfed by an interaction with sheep, which shifted the

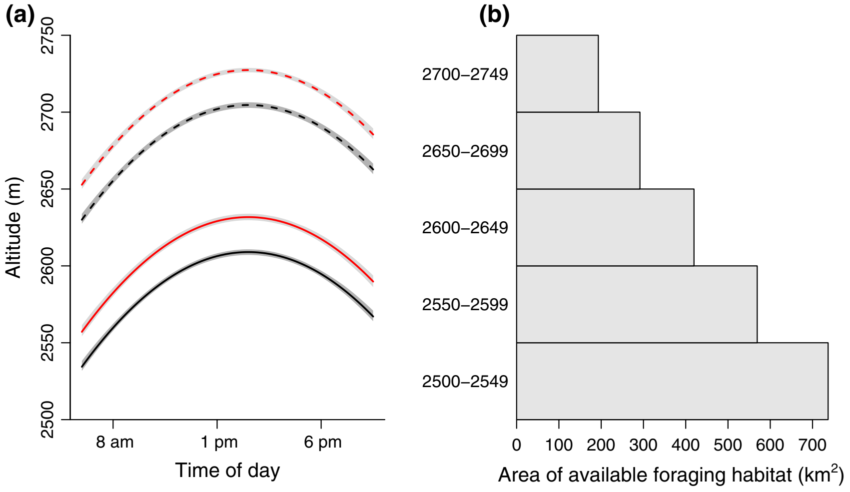

Fig. 4 (a) Predicted mean daily variation in altitude use in the presence (dashed lines) and absence of sheep (solid lines), both in the present climate (black lines) and a 5 °C warmer climate (red lines). Predictions were made using the most parsimonious structural equation model (i.e. that with the lowest Akaike Information Criterion), and using mean values for all predictors other than time of day. Grey shaded areas are 95% confidence intervals (Efron & Tibshirani, 1991). (b) Variation in available foraging habitat (see text for details), across the European Alps, in different 50 m altitudinal bands which encompass the entire summer altitudinal range of this population.

altitudinal range of chamois dramatically upslope. This finding highlights the importance of considering how factors such as competition and disturbance shape the realised niche of a species, to understand its response to climate change. Most studies of future distribution change use observed distributions to assess climate suitability (e.g. Pearson & Dawson, 2003; Araujo & Pearson, 2005); however, apparent climate suitability might be shaped and, critically, narrowed by the presence of competitors. Range-shift predictions should be made in the light of potential changes in community composition and, thus, competition. Our work also reveals the complexity that can arise as a result of multiple potential behavioural responses to climatic variation. We show that chamois respond to variation in temperature by adjusting their activity budgets, as well as by migrating between different altitudes. This behavioural flexibility may significantly influence how species respond to anthropogenic climate change.

Temperature exerted a direct influence over chamois altitude use: when ambient temperature was higher, for a given time of day, chamois moved to higher altitudes (Fig. 3b). However, this effect was relatively modest: our models suggest that, during the study period, chamois moved on average 8–11 m upslope per 1 °C increase in air temperature (see Fig. 3b). For the most extreme climate change scenario for the region, a 5 °C increase in mean summer temperature by 2100, our model predicts a relatively modest increase in 15–30 m in the mean altitudinal range of chamois (Fig. 4a). In contrast, the presence of sheep had a much stronger effect on altitudinal migration (Table 1, Fig. 3a, 4a). After the introduction of sheep into the study area, chamois moved on average 96 m upslope, shifting to an entirely novel altitudinal range. If the effects of sheep and climate change were to act concurrently in the future, this upslope shift could be even larger – 112–125 m – entailing a 55% reduction in foraging habitat across the Alps (Fig. 4a). There is frequently considerable overlap among ranges of wild ungulate species (Harris & Miller, 1995; Hibert *et al.*, 2010) but the presence of livestock species is known to cause displacement of many wild ungulate populations. In mountainous areas, wild ungulates may move to higher altitudes when disturbed, which can result in dietary changes and even bring them into competition with other wild species (Shrestha & Wegge, 2008a,b; Hibert *et al.*, 2010). However, to our knowledge, such a pronounced effect on a population's altitudinal range has not been documented previously. Range displacement of wild ungulates by livestock can be caused by direct, visual, or acoustic disturbance (Mattiello *et al.*, 2002), foraging competition (Garcia-Gonzalez *et al.*, 1990) or perceived risk of disease transmission (Ezenwa, 2004). Due to high dietary overlap between chamois and sheep, resource competition could be the mechanism of disturbance (Rebollo *et al.*, 1993; La Morgia & Bassano, 2009). Some authors have suggested that disturbance from livestock generally results from a perceived predation threat due to the presence of humans and other animals associated with them (Bagchi *et al.*, 2004). However, range displacements can also occur where livestock are not attended by humans or guardian species (Shrestha & Wegge, 2008a,b). In a different population, chamois were disturbed by sheep even in the absence of sheep-dogs, but this effect was stronger if dogs were present (Chirichella *et al.*, 2013). In our study area, where sheep were only periodically associated with shepherds and dogs, the mechanism of disturbance is unclear. Regardless, our finding highlights the strong influence that interspecific interactions, as well as human activities, can exert on species distributions.

Temperature also influenced chamois activity budgets: chamois allocated less time to foraging when it was warmer, for a given time of day (Fig. 3d). Clearly, both altitudinal migrations and regulation of activity budgets can be used to ameliorate the consequences of substantial diurnal fluctuations in temperature. That chamois limit their activity during hotter periods could reduce their need to undertake dramatic changes in elevation, which are likely to entail a high energetic cost (Fancy & White, 1985; Dailey & Hobbs, 1989), to cope with higher temperatures. Eurythermic species, such as chamois, could be more adaptable to a changing climate than stenothermic (adapted to a narrow range of temperatures) species such as Alpine ibex. Ibex exhibit much more pronounced altitudinal and activity budget responses to temperature than chamois do (Grignolio *et al.*, 2004; Aublet *et al.*, 2009). To date, the relative contributions of different thermoregulatory behaviours in responding to climate change have not been considered. The presence of sheep also influenced chamois activity budgets, albeit weakly; when sheep were present chamois tended to spend slightly more time foraging (Table 1). This could be due to a change in their foraging habitat following their movement upslope; following the introduction of sheep, chamois tended to use more sparsely vegetated areas, compared to the low-altitude alpine meadows utilised previously. As such, chamois may have had to forage for longer, spending more time moving between patches, in order balance their energy budgets (Charnov, 1976). Reductions in forage plant density with similar increases in altitude have been demonstrated previously in the Alps during summer (Aublet *et al.*, 2009). We found that unscreened temperature explained more variation in time spent foraging than screened temperature did. The absorption of solar radiation is thought to play a key role in the heat balance of endotherms such as mammals and birds due to the presence of insulatory layers of fur or feathers (Porter *et al.*, 2000). Our results suggest that the absorption of solar radiation could form an important sensory cue for this species, controlling their patterns of behavioural thermoregulation.

This study shows that short-term intensive behavioural studies can uncover important patterns of relevance to global change biology. We highlight two important issues: (i) the significance of considering how competition affects a species' niche and (ii) the potential role of behavioural flexibility in species responses to climate change. Firstly, our findings show the importance of considering how competition and disturbance shape the realised niche of a species, to understand the constraints on future range change. Despite it being well understood that the distributions of many species are not in equilibrium with climate (e.g., Svenning & Skov, 2004; Araujo & Pearson, 2005; Monahan, 2009), most species distribution modelling techniques focus on only the observed distributions of species, which are subject to the constraints of dispersal and interactions with other species. As such, future range-shift projections which do not quantify the influence of biotic factors on a species' niche are likely to be erroneous because community composition and competition are likely to change in future if species respond to different aspects of a changing climate (Klanderud & Totland, 2005). We propose that it is vital to understand how factors such as competition contribute to a species' realised niche to fully appreciate the potential constraints on future range change and make realistic range-shift predictions. Furthermore, our findings highlight a novel management tool; the potential impacts of climate change could be ameliorated by the appropriate management of the species responsible for negatively affecting vulnerable populations. The value of controlling certain species, particularly predators, to aid the recovery of threatened and declining species is already well acknowledged (Lessard *et al.*, 2005). However, such a management strategy has not been explored in the context of ameliorating negative impacts of climate change. This could be particularly applicable in study systems where an interspecific interaction has restricted the range of a relatively eurythermic species and where control of the responsible species' distribution is feasible, as is the case here with livestock. Future work should also examine the feasibility of controlling wild competitors to expand the realised niche of vulnerable species.

Secondly, our results reveal that predictions made from behavioural observations are likely to be highly disparate from, and potentially more informative than, those from traditional species distribution models (SDMs), due to the potential for multiple behavioural responses to climate change. The predicted increase of 15–30 m in the mean altitudinal range of chamois in response to 5 °C of climate warming (Fig. 4a) would entail habitat losses: in the European Alps, suitable foraging habitat starts to become more limited at higher elevations (Fig. 4b). This could necessitate individuals to adapt how they forage and could lead to population declines (see next paragraph for further discussion). However, an SDM-type approach, which assumes that chamois will track the movement of their current thermal niche upslope, would predict a response at least 27 times greater: an upslope shift of approximately 830 m [assuming an average 0.6 °C/100 m lapse rate, the rate of temperature change with increasing elevation, in the Alps during summer (Kirchner *et al.*, 2013)]. The result of such a change would be dramatic: in this study area there is currently no suitable foraging habitat 830 m upslope. However, the SDM-type predictions assume that chamois will only respond by shifting their range upslope. In fact, our findings reveal that altitudinal migration does not play a primary role in behavioural thermoregulation in this species, due to considerable plasticity in activity budgets. Behavioural flexibility underpins the response of chamois to diurnal temperature variation and could play an important role in their long-term response to climate change. Behaviours could help buffer the impacts of climate change on ectotherms (Kearney *et al.*, 2009) and could also play a role for endotherms (Huey *et al.*, 2012). Our findings highlight that endotherms are not restricted to shifting their ranges in the face of a changing climate; behavioural thermoregulation is an overlooked, but potentially important, component of how they respond.

Despite the potential value of behavioural studies, it is uncertain how short-term behavioural variation, such as the diurnal behavioural variation observed here, translates into long-term behavioural change. Our model predicts that chamois would spend as much as 10% less time foraging in a 5 °C warmer climate. This would undoubtedly have a considerable negative impact on the ability of individuals to acquire sufficient resources for growth and reproduction, which could have important influences on body condition and, in turn, population dynamics (Ozgul *et al.*, 2009, 2010). Indeed, it has been suggested that long-term body mass declines in chamois could be a result of temperature-mediated reductions in foraging time (THE Mason, SG Willis, R Chirichella, M Apollonio, PA Stephens, In review). However, in the future, species might adapt how they perform behaviours, for instance by adjusting the timing of foraging bouts. Individuals could forage more in the early hours and evenings, when it is cooler, and spend even less time active during the middle of the day. Such alterations would, of course, be subject to trade-offs with other factors, such as increased vulnerability to predation if foraging effort was increased at dawn and dusk. SDMs, which predict temporal distributional change based on the current relationship between distribution and climate, are similarly limited in their ability to project into the future: spatial variation in climate-distribution relationships may not translate into temporal change (e.g. Thuiller, 2004; Lawler *et al.*, 2006). However, behavioural studies can at least shed light on the constraints on range-shift responses to climate change. We show that, in the absence of a different, long-term mechanism of range change, high altitude populations of chamois will not track the upslope movement of their thermal niche.

In summary, variation in temperature exerts an influence over chamois behaviour but diurnal altitudinal migration in this species is strongly disturbed by the presence of other species. A lack of understanding of the factors that shape a species' realised niche, which might result in a species underfilling its climatic niche (Sunday *et al.*, 2012), could lead to projections of climate change impacts that are very different to what eventuates. Our findings bring to light a novel means by which to adapt the management of susceptible species to cope with climate change, namely that for species where competition or disturbance has affected their available niche, controlling competitors could ameliorate climate impacts. Finally, we find that behavioural flexibility, such as temperature-mediated variation in activity budgets, could play an important role in how some species respond to climate change. Our study shows that research into how species habitually respond to climatic and environmental variation has the potential to contribute greatly to our understanding of how species respond to anthropogenic climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. The set of structural equation models with ecologically sensible combinations of predictors that were fitted in the modelling procedure. The response variables are altitude use (Altitude), local temperature ($\text{Temp}_{\text{local}}$), and time spent foraging (Foraging). The predictors are time of day (Time), time of day^2 (Time^2), presence of sheep (Sheep), fixed altitude temperature ($\text{Temp}_{\text{fixed}}$), $\text{Temp}_{\text{local}}$, $\text{Temp}_{\text{local}}{}^2$, Altitude, and group size (Group). An 'x' indicates the presence of a predictor effect on a given response variable. Each model was fitted with both unscreened temperature as $\text{Temp}_{\text{local}}$ and screened temperature as $\text{Temp}_{\text{local}}$, meaning that 56 different models were fitted in total. K indicates the number of parameters in each model, which includes regression coefficients, intercepts for each variable, variance parameters for each variable, and covariance parameters between different variables.

Table S2. The set of 'acceptable' structural equation models – those which fit the observed data well [as demonstrated by nonsignificant chi-square and root mean square of approximation (RMSEA) values]. The response variables are altitude use (Altitude), local temperature ($\text{Temp}_{\text{local}}$), and time spent foraging (Foraging). The predictors are time of day (Time), time of day^2 (Time^2), presence of sheep (Sheep), fixed altitude temperature ($\text{Temp}_{\text{fixed}}$), $\text{Temp}_{\text{local}}$, $\text{Temp}_{\text{local}}{}^2$, Altitude, and group size (Group). Standardised effect sizes of each predictor shown. Chi-square test statistic, RMSEA ± 95% confidence intervals and *P*-values for each metric are shown. Nonsignificant *P*-values (>0.05) for these metrics indicate a well-fitting model. K indicates the number of parameters in a model, which includes regression coefficients, intercepts for each variable, variance parameters for each variable and covariance parameters between different variables. Differences in Akaike Information Criteria (ΔAIC) are shown.