Title: Joint effects of weather and interspecific competition on foraging behaviour and survival of a mountain herbivore

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Abstract

Weather variations have the potential to influence species interactions, although effects on competitive interactions between species are poorly known. Both weather and competition can influence foraging behaviour and survival of herbivores during nursing/weaning, a critical period in the herbivore life cycle. We evaluated the joint effects of weather and competition with red deer *Cervus elaphus* on the foraging behaviour of adult female Apennine chamois *Rupicapra pyrenaica ornata* in summer, and on winter survival of chamois kids. High temperature and low rainfall during the growing season of vegetation had negative effects on bite rate. Effects of weather were greater in forb patches, including cold-adapted, nutritious plants of key importance to chamois, than in graminoid ones. Our results confirm previous indications of a negative effect of competition on bite rate of female chamois and on kid survival. Furthermore, harsh weather conditions and competition with deer had additive, negative roles on foraging behaviour and survival of chamois.

Growing temperatures are expected to influence distribution, growth and/or nutritional quality of plants; competition would reduce pasture quality and food availability through resource depletion. Both factors would limit food/energy intake rates during summer, reducing survival of the youngest cohorts in winter. We suggest that interspecific competition can be an important additive factor to the effects of weather changes on behaviour and demography.

Key-words: chamois; foraging behaviour; global changes; interspecific interactions; resource exploitation; ungulates.

Introduction

Weather can have strong effects on the behaviour and the ecology of wild animals, influencing individual, population and ecosystem-level processes (e.g., Post et al. 1999, 2009; Conradt et al. 2000; Roy et al. 2001; Chen 2011; Sheridan and Bickford 2011; van Beest and Milner 2013; Mason et al. 2014a). Long-term changes in weather patterns can alter relationships between species. Interactions between sympatric species may buffer (Wilmers and Getz 2005) or amplify (Mason et al. 2014a) the effects of weather changes on a focal species. For example, predatory action by wolves can increase availability of carcasses for scavengers, thus mitigating for a late-winter reduction of carrion abundance triggered by growing temperature and the resulting earlier snow-melt (Wilmers and Getz 2005). Alternatively, long-term weather changes may modify consumer-resource dynamics and patterns of interactions between species, disrupting mutualistic relationships, altering parasite-host dynamics or modifying the intensity or timing of trophic interactions (Traill et al. 2010). However, so far, interactions between long-term patterns of weather changes and competitive interactions have been relatively neglected (but see birds: Stenseth et al. 2015; Wittwer et al. 2015). Climate represents the average, long-term pattern of weather conditions. Assessing biological responses to weather variation can help to predict relevant effects of climatic changes (e.g., Roy et al. 2001; Mason et al. 2014a). Weather and interspecific competition may have synergistic or additive effects on the behavioural ecology of species. For example, the negative effects of weather on a focal species may be greater if a competitor is present or, alternatively, they could impose independent pressures. Understanding mechanisms through which weather influences the behaviour and ecology of species is fundamental to building explicit predictions.

The effects of weather dynamics should be particularly detectable in delicate, mountainous ecosystems (Engler et al. 2010; Pauli et al. 2012; Elsen and Tingley 2015). Drought stress and high temperatures are expected to limit the nutrient supply to plants and to reduce their digestible protein content (e.g., Jonasson et al. 1986; Marshal et al. 2005). In turn, food and energy intake of female herbivores during nursing/weaning periods would be affected, resulting in negative effects on growth and survival of offspring (e.g., Clutton-Brock et al. 1984; Festa-Bianchet and Jorgenson 1997; Pettorelli et al. 2007; Therrien et al. 2008). Exploitation of resources by competitors could further reduce the availability of food, emphasising the negative effects of weather.

High elevation meadows within the Central Apennines present a useful case study of the interacting effects of weather dynamics and interspecific competition between herbivores. Specifically, these areas: (1) are habitat for diverse communities of vegetation, including a range of nutritious but cold-adapted forbs; (2) are home to the Apennine chamois *Rupicapra pyrenaica ornata*, a rare subspecies recognised to be vulnerable to extinction (Herrero et al. 2008); and (3) are currently witnessing an expansion of reintroduced red deer *Cervus elaphus*, which compete with chamois (Lovari et al. 2014; Ferretti et al. 2015; see below). Apennine chamois are reliant on high-quality vegetation belonging to cold-adapted, legume-dominated forb patches, growing on terrain subject to prolonged snow cover (Ferrari et al. 1988); consequently, these mountain ungulates might be particularly vulnerable to warmer temperatures. In the Pyrenees, winter survival of adult females of Pyrenean chamois *R. pyrenaica pyrenaica* was positively influenced by high precipitation and low temperature in the previous spring (Loison et al. 1999a). Furthermore, in the closely-related Northern chamois *Rupicapra rupicapra*, high temperature in spring-summer has been suggested to reduce activity levels and time spent foraging, as well as body mass (Garel et al. 2011; Rughetti and Festa-Bianchet 2012; Mason et al. 2014a-b; Brivio et al. 2016). Conversely, Loison et al. (1999a) reported that winter survival of adult female Alpine chamois *R. r. rupicapra* was negatively affected by high precipitation and low temperatures in the previous spring.

The recent expansion of reintroduced red deer in the Apennines has resulted in areas where the two species are sympatric and areas where chamois, as yet, occur in the absence of red deer. This presents the opportunity to contrast chamois behaviour between neighbour areas with and without red deer, subject to the same weather dynamics, yielding a ‘natural experiment’ to assess the impacts of weather and competition on chamois behaviour and survival. Dietary overlap between red deer and chamois has been detected in several mountainous massifs (Schröder and Schröder 1984; Homolka and Heroldovà 2001; Bertolino et al. 2009; Lovari et al. 2014; Redjadj et al. 2014). In our study areas, summer food resources shared by red deer and chamois range from nutritious, cold-adapted forbs, to less nutritious graminoids; dietary overlap can exceed 90% (Lovari et al. 2014). Resource exploitation by red deer has been shown to affect bite rate of female chamois, through negative effects on vegetation availability (Lovari et al. 2014; Ferretti et al. 2015). Presumably, variation in temperature and rainfall throughout summer should also have an effect on chamois foraging behaviour. Low rainfall and high temperatures would limit the nutrient supply to plants and, in turn, their digestible protein content, reducing bite rate through a greater handling (chewing) time (e.g., Shipley and Spalinger 1992; Wilmshurst et al. 1999; St. Louis and Côté 2012). In particular, we predict that: (*i*) the bite rate of female chamois is negatively affected by higher temperature and lower rainfall during the vegetative growth season; and (*ii*) effects of temperature on bite rate are greater in patches dominated by cold-adapted forbs than in those dominated by graminoids. In addition, given its strong link with summer foraging by females, we consider winter survival of chamois offspring (Ferretti et al. 2015). In summer, nutritious forbs are selected by chamois (Ferrari et al. 1988; Ferretti et al. 2014; Lovari et al. 2014) and are eaten in comparable proportions by red deer also (Lovari et al. 2014). In turn, deer grazing could affect mainly nutritious food patches. As a result, the magnitude of the negative effects of harsh weather on the best food resources for chamois, and thus on their bite rate and survival, could be greater under competition with deer than in competition-free areas. Thus, we evaluated (*iii*) whether effects of weather variations on bite rate of female chamois and survival of chamois kids were increased under interspecific competition with red deer and used projection matrices to compare the effects of survival differences between sites with/without deer.

Material and methods

Study areas

Our study was conducted in two areas of Abruzzo, Lazio and Molise National Park (ALMNP, central Italy). Site A (chamois-deer site) was located in upper Val di Rose (*c.* 1700-1982m a.s.l, 41.745108N, 13.916351E, WGS 84); Site B (chamois-only site) included the upper meadows of Mt. Meta (*c.* 2100-2242 m a.s.l., 41.691142N, 13.936764E). The two sites were *c.* 5.5 km from one another. The areas have a temperate oceanic bioclimate, with snow cover lasting from late November to late May-early June (Bruno and Lovari 1989). Both sites lie on calcareous ground, with two main vegetation types grazed by chamois: palatable graminoids (mainly *Festuca* spp., Site A: 35.5%, Site B: 38.7%) and forb-dominated vegetation, the best food patches for chamois (Ferrari et al. 1988; e.g. *Trifolium thalii*, *Ranunculus apenninus*, *Plantago atrata*, *Anthyllis vulneraria*, Site A: 15.2%, Site B: 24.5%, Ferretti et al. 2015). Sites included also patches dominated by unpalatable graminoids (*Brachypodium genuense*, Site A: 24.9%, Site B: 1.0%) and rocks/screes with sparse vegetation (Site A: 24.4%, Site B: 35.8%, Ferretti et al. 2015). We observed foraging behaviour of female chamois in summers 2010-2013 in Site A, and in summers 2012-2013 in Site B. During our study, depending on year, a minimum of 60-85 chamois were present in Site A and 78-98 individuals in Site B (Lovari et al. 2014, Ferretti et al. 2015). Only 4-6 adult male chamois (and no females, kids or subadults) were present in Site B in 1970-1980's (Lovari 1977; S. L. pers. obs.). Since then, chamois numbers have increased in Site B, while they have declined by *c.* 50% in Site A (Lovari et al. 2014). Data on emigration movements of female ungulates are few and approximate, but indicate that emigration is an infrequent event (Loison et al. 1999b; Bocci and Lovari 2010). Therefore, the female segment of our herds can be considered as a closed one. Wolves *Canis lupus*, brown bears *Ursus arctos*, and golden eagles *Aquila chrysaetos* also occurred in both sites. For further details on study areas, see Lovari et al. (2014) and Ferretti et al. (2015). Weather data (mean daily temperature; daily rainfall) were provided by Servizio Idrografico e

Maregrafico - Regione Abruzzo (Passo Godi-Scanno station, 41.837028N, 13.929499E, 1570 m a.s.l.), *c.* 10 and 15 km far from Site A and B, in a straight line, respectively.

Behavioural observations

Female Apennine chamois give birth on cliffs between May and June; herds with adult females, immatures and kids graze on upper meadows from summer (i.e. after snowmelt and births) to early winter (Lovari and Cosentino 1986; Bruno and Lovari 1989). Nursing peaks up to August (unpublished data; cf. Ruckstuhl and Ingold, 1994, for *R. rupicapra*). We recorded foraging behaviour of adult female (i.e. > 3 years old, Lovari 1985) chamois in summer (mid-July - late August). Adult female chamois were observed from vantage points, at a distance of 30-200 m, from dawn to dusk. The foraging behaviour of chamois was recorded through focal animal sampling (Altmann 1974), in 10-min bouts, divided by 1-min sampling intervals (Ruckstuhl et al. 2003; Lovari et al. 2014, Ferretti et al. 2014, 2015). Each 1-min focal sample was followed by a data recording interval of 5-10 seconds (Bruno and Lovari, 1989; Ruckstuhl et al. 2003). We recorded the number of bites to vegetation/min (bite rate, an index of food intake rate; Bruno and Lovari 1989; Ruckstuhl et al. 2003): a bite was identified by seeing the chamois removing a bite of vegetation or by the distinct jerking motion of its head (Bruno and Lovari 1989). When necessary, 10×50 binoculars and 20-60× spotting scopes were used to allow visibility of the mouth of chamois. We assessed the vegetation used by the focal animal (forbs; palatable graminoids) after it vacated the area (Ferretti et al. 2015). At the beginning of each focal bout, we also assessed visually the extent of rock cover in a 5 m radius around the focal animal (0-25%; 25-50%; >50%), by considering the chamois torso length as a reference (cf. Frid 1997).

We carried out short-term (10 min/ind) observation bouts on unmarked individuals. We made all efforts to collect data on different individuals in the same day to reduce pseudoreplication. We recorded data on individuals that could temporarily be distinguished by their respective positions on the slope (Lovari et al. 2014; Ferretti et al. 2015). Observation bouts were discarded when the focal animal disappeared from sight after < 5 min. We obtained 534 sampling bouts (Area A: $n = 357$, in 2010-2013; Area B: $n = 177$, in 2012-2013).

In each study area, we assessed the number of kids, yearlings and subadult/adult chamois in mixed herds (i.e. with females, yearlings, and kids), by considering the maximum number of individuals observed at the same time during behavioural observations, divided by age class. We considered the following age classes (kids: 0 years old; yearlings: 1 year old; subadults: 2–3 years old; young adults: 4–5 years old; mature adults: >5 years old, Lovari 1985). For each study area, we calculated (see above) yearlings:kids (in the previous year) ratios as an approximation of kid winter survival (maximum number of yearlings in July/maximum number of kids the year before, in summer, Ferretti et al. 2015).

Data analyses

We evaluated the effects of weather and presence of deer on bite rates of female chamois through linear mixed effect models (Crawley 2007). Variation in temperature and rainfall influence development, growth and nutritional value of plants, affecting the nutritional quality of pasture for herbivores in the following weeks/months (e.g. Shackleton and Bunnell 1987; Pettorelli et al. 2007). In turn, the foraging behaviour of herbivores would be influenced *via* effects on vegetation. In our study areas, snow melt usually occurs in late May-early June and most ground is without snow at the beginning of June. Accordingly, we evaluated whether bite rates were influenced by mean temperature and total rainfall during the 45 days leading up to the foraging observations, thus including a period when the ground was directly exposed to weather. To evaluate the potential effects of weather changes at shorter temporal scales, we also calculated mean temperatures and total rainfall during the 30 and 15 days leading up to observations. Where relevant, the presence or absence of deer was included in models by including site (A, deer present; B, deer absent) as a fixed effect.

In a first set of models, we evaluated the effects of weather variability on bite rate of female chamois in the deer-present area (Site A), for which data were available for a longer sampling period, i.e. 2010-2013. We calculated different sets of models for each temporal scale (15, 30 and 45 days). The response variable was the average number of bites per minute, taken in each 10-min focal bouts. Our full models included the following predictors (Table 1): mean temperature and total rainfall in the 45 (30 or 15) days before observation date; time of day (allowing for a quadratic effect, as we did not expect a monotonic increase or decrease in foraging through the course of the day); extent of rock cover around the animal (0-25%; 25-50%; >50%); and vegetation type (forb-dominated patch; graminoid-dominated patch, Ferretti et al. 2015). Plants of the different vegetation types have different heights (typically< 10 cm tall in forb-dominated patches and > 10 cm in graminoid-dominated patches, see also Ferretti et al. 2014). The inclusion of vegetation type among predictors is expected to allow a control for the effects of plant height, which should influence bite rates. To evaluate whether effects of weather differed between vegetation types, we also included the interaction terms: mean temperature × vegetation type, and total rainfall × vegetation type. Date was included as a random factor to account for unexplained differences in feeding intensity on different days (Ferretti et al. 2015). We initially included date (i.e. day of year) as a linear predictor, also. However, each year, date was highly correlated with temperature (Pearson's rho = 0.877-0.985). Consequently, date was not included among the predictors in our final models (but our conclusions were unaffected relative to those drawn from models which included date as a predictor; see Supplementary Material 1-2). Additionally, we calculated models including date but not temperature among predictors, but the effect of date was not supported (see Supplementary Material 3-4). Temperature and, especially, rainfall patterns differed greatly across years (Supplementary Material 5). In particular, only 6 days with rainfall were recorded in June-mid-July 2012, which is inconsistent with the pattern observed in the previous 24 years (1990-2013: median = 13 days, interquartile range = 11.3-18.3), with no rain from1-22 July and total rainfall c. 40% lower than the mean over 1990-2013 (Supplementary Material 5). As weather effects were an important focus, we did not include year among predictors, to avoid subsuming the effects of weather variables on bite rates into the effects of year. We selected among all models using the 'dredge' function in the R package 'MuMIn' (Bartoń 2012), fitting all possible models (*n* = 312). Model selection used Akaike's Information Criterion corrected for small sample sizes (AIC_c): models were retained for inference if they had $\Delta AIC_c \leq 6$ units, and if their AIC_c value was lower than that of any simpler, nested alternative (Richards 2008; Richards et al. 2011). A ΔAIC_c threshold of 6 has been shown to provide a high probability (≥ 0.95) that the model with the lowest Kullback-Leibler distance is retained (Richards 2008; Richards et al. 2011). Model coefficients were estimated using the 'confint' function (Bartoń 2016).

We then compared the two study sites through linear mixed models, using data collected in 2012-2013, i.e. the sampling period for which data had been collected in both sites, to evaluate whether the effects of weather conditions on bite rate of female chamois differed between areas also grazed/ungrazed regularly by red deer. In addition to the predictors and random effects used in the 1-site models, we included also the fixed effects of site and those of the interactions: mean temperature × site and total rainfall × site (Table 1). Model selection was conducted as above (*n* = 1128 models). Variance inflation factors associated with linear predictors were < 2; residuals showed no obvious deviations from normality/homoscedasticity of residuals or autocorrelations (see Supplementary Material 6 for model diagnostics).

Inferring the potential demographic impact of competition

Using our increased sample size (relative to that analysed by Ferretti et al. 2015), we compared kid survival between years and across areas with and without red deer. We used indices of survival of kids born in 2011, 2012 and 2013 (i.e. the maximum number of individuals observed at the same time, during behavioural observations; for n. kids born in 2011, in Site B, data from Latini et al. 2011) as response variables in generalized linear models with binomial errors (Crawley 2007). We coded the response variable as follows. Kid survival was modelled as a Bernoulli process in which the number of successes (survivals from kid to yearling) was determined as the number of yearlings counted in year t+1, and the number of failures (kid mortalities) was determined as the number of kids counted in year t, less the number of yearlings counted in year t+1 (see also Ferretti et al. 2015). Study area and Year were the predictors. Our full model for the index of kid survival included site and year as predictors; moreover, in addition to analyses done by Ferretti et al. (2015), we included the interaction site × year to test whether, in the winter following the drought observed in 2012, kid survival decreased in both sites or only in the deer-present one (Table 1); model selection was conducted as described above.

We constructed female-only, post-breeding matrix models for chamois herds in Site A and B, using local data on birth ratio (maximum number of kids:maximum number of females observed at the same time during behavioural observations, years pooled, Site A: 2010-2014, Site B: 2012-2014) and kid survival (Lovari et al. 2014; Ferretti et al. 2015), and assuming a 1:1 sex-ratio (cf. Bocci et al. 2010; Devenish Nelson et al. 2010). Information on adult survival is not available for Apennine chamois and, thus, we took estimated survival rates from a closely related species (Alpine chamois *R. rupicapra*, Corlatti et al. 2012; see also Loison et al. 1994). Wolves occurred in both our study sites, but were absent from the Alpine study areas (Loison et al. 1994; Corlatti et al. 2012), which could have influenced chamois survival in our study sites. However, in our study areas predation of wolves on Apennine chamois appears to be low (Patalano and Lovari 1993; Grottoli 2011). In our study areas, the escape terrain of chamois is hardly accessible to wolves (Baruzzi et al. 2017); the availability of other, abundant and more easily accessible large prey (wild boar, red deer and roe deer, Patalano and Lovari 1993; Grottoli 2011), as well as the overall lowest density of chamois, concentrated on only a few suitable areas (Ferrari et al. 1988) in respect to the Alps (Alpine chamois: Tosi and Pedrotti 2003; Apennine chamois: Lovari and Bruno 2003) may discourage predation on chamois. Likelihood of kid survival (P_x) was estimated following Devenish Nelson et al. (2010), using the "dbinom(events,trials,P_x)" function in R. In the transition matrix ($\mathbf{A}_i$), we considered 5 stage classes: kids, yearlings, 2 years old, 3 years old and adults (> 3 years old, cf.

Lovari 1985). The female-only birth ratio used was 0.32; survival values used were 0.90 (yearlings), 0.91 (2-3 years old individuals), 0.92 (adults). Population growth (λ_i) was determined from the dominant eigenvalue of $\mathbf{A}_i$ using point estimates of each matrix element for survival (cf. Devenish Nelson et al. 2010). Ninety-five% confidence intervals were determined using a resampling approach: λ_i was estimated from 10,000 replicate projection matrices, with each element drawn from its corresponding likelihood distribution (Wisdom et al. 2000; Devenish Nelson et al. 2010). For each site, we also estimated S_0, i.e. the index of survival which would lead to $\lambda_i = 0$.

Results

Foraging behaviour

Our analysis of factors affecting bite rate in the presence of competition from deer showed support for a positive effect of rainfall in the previous 45 days, in forb-dominated patches (Tab. 2a-3; Fig. 1). Bite rate decreased with increasing rock cover (Tab. 2a-3).

When the factors influencing bite rate were assessed across the sites with and without deer, there was support for the effects of site, vegetation type, temperature, rainfall, rock cover and time of day (Tab. 2b-3; Figs. 2-3). In particular: (*i*) the bite rate was greater in the deer-free area than in the area where deer were present; (*ii*) high temperature in the previous 45 days had a negative effect on bite rate in both sites, especially in forb patches; (*iii*) low rainfall in the previous 45 days was followed by a decrease in bite rate in both sites (Tab. 2b-3). Bite rate was greater in forb-dominated patches than in graminoid-dominated ones and decreased with increasing rock cover (Table 2-3).

Yearling:kid ratio and demographic parameters

In Site A, the index of kid survival varied from 0.10 (2012) to 0.36 (2013). In Site B, this index ranged from 0.40 (2012) to 0.60 (2013). GLMs found strong support for an impact of site (with or without deer), and weak support for the additive effects of year (Table 2c). The index of kid survival was greater in the absence of deer and lowest in the winter following the 2012 drought, when it was *c*. 70% (Site A) and 30% (Site B) lower than in the other years, although the effect of year was only included in the best model (Fig. 4; Table 2c).

Matrix population models suggest that kid survival of approximately 0.36 would be required for a self-sustaining population. Kid survival in the absence of deer (Site B) appeared to exceed this requirement with a likelihood of 0.987; the best estimate of kid survival was 0.49, corresponding with a population growth rate of $\lambda_B = 1.02$ (Fig. 5). By contrast, in the presence of deer (Site A), kid survival lay below the threshold required for stability with a likelihood of 0.950. The best estimate of kid survival was 0.27, corresponding to a population growth rate of $\lambda_A = 0.98$ (Fig. 5). This growth rate would lead to a reduction of 50% over a period of *c*. 35 years.

Discussion

Previous studies showed negative effects of resource exploitation by red deer on the foraging behaviour and survival of Apennine chamois (Lovari et al. 2014; Ferretti et al. 2015), but relationships between competition and weather were not clear. Here we suggest a negative effect of high temperature and low rainfall on the foraging behaviour of chamois. Higher temperatures and lower rainfall negatively influenced the bite rate of female chamois in the nursing period. Winter survival of chamois offspring was the lowest after 2012's early summer drought. The effects of weather factors appear to be additive to the negative impacts of competition with red deer.

Foraging behaviour and survival of mountain herbivores are expected to be hampered by food depletion, especially in the warm months (e.g., Festa-Bianchet 1988; Côté and Festa-Bianchet 2001; Pettorelli et al. 2007). Weather affects growth, viability, distribution and protein content of plants (e.g., Jonasson et al. 1986; Schöb et al. 2009; Gottfried et al. 2012) which, in turn, influence foraging behaviour of herbivores (e.g., Spalinger and Hobbs 1992; Ruckstuhl et al. 2003; Moquin et al. 2010; St. Louis and Côté 2012). The bite rate of female Apennine chamois was negatively affected by high temperatures and lower rainfall in previous weeks. These results may serve as an index of potential effects of climatic changes. Drought stress and high temperature reduce the digestible protein content of plants (e.g., Jonasson et al. 1986; Marshal et al. 2005; Zamin et al. 2017). In turn, a less nutritious and more fibrous food would require greater mastication costs, with a higher chewing time, reducing bite and energy intake rates (e.g., Shipley and Spalinger 1992; Wilmshurst et al. 1999; St. Louis and Côté 2012). Additionally, high temperatures could accelerate plant senescence, which would further limit bite rate, increasing handling time (Parsons et al. 1994). In graminoid-dominated patches, the size of grasses (typically > 10 cm tall) is greater than that of plants growing in forb-dominated patches (typically < 10 cm tall), which could explain why the bite rate of female chamois was lower in the former than in the latter (Parsons et al. 1994; see Lovari et al. 2014; Ferretti et al. 2014, 2015). Additionally, the higher nutritional content of forbs (Ferrari et al. 1988) could determine lower mastication costs relative to grasses (see also Parsons et al. 1994), in turn enhancing bite rate. Warmer temperature and lower rainfall had a bigger impact on bite rate of female chamois foraging in forb than in graminoid patches, suggesting that the former are more vulnerable than the latter to high temperature and lower rainfall. Cold-adapted forbs include legumes and other dicotyledonous plants, affected by growing temperatures, limited water content and snow cover persistence (Ferrari et al. 1988; Harte and Show 1995; Schöb et al. 2009). Furthermore, rising temperatures are likely to reduce snow cover quantity and persistence, which could be detrimental to snow-bed vegetation (e.g., *Trifolium thalii*-dominated communities), the key-summer resource for chamois (Ferrari et al. 1988; Schöb et al. 2009; D'Angeli et al. 2011).

Mason et al. (2014b) suggested that temperatures during the green-up season and population density limited the body mass of yearling Alpine chamois, because both avoidance of heat stress and intra-specific competition can alter feeding patterns and limit food intake. Indirect effects of environmental changes on body mass were not explained *via* effects on vegetation productivity/phenology, indexed by NDVI metrics. However, effects of growing temperature/population density on nutritional quality of pasture cannot be ruled out through NDVI indices (because NDVI indices might be unresponsive to shifts in the relative abundance of relatively palatable and unpalatable species). Our results suggest that weather – and particularly hot growth-season temperatures – could affect bite rates and, indirectly, chamois kids' body mass. Additionally, higher temperatures may alter the feeding pattern by limiting time spent foraging in the warmer part of the day, to avoid heat stress (Mason et al. 2014a-b), further limiting food/energy intake.

Our findings are consistent with additive mechanisms of action by weather and interspecific competition on the availability of nutritious pasture for chamois. If occurring consistently throughout years, higher temperatures can decrease the availability of high-quality growing vegetation, and/or lead to a mismatch between green-up and birth peaks of herbivores (Pettorelli et al. 2007). Upward shifts of plant communities have been documented throughout Europe, with thermophilic species replacing cold-adapted plants in high altitude grasslands (Gottfried et al. 2012; Pauli et al. 2012; Stanisci et al. 2015). Over the past 30 years, nutritious plants grazed by chamois, e.g. *Trifolium thali*-dominated communities, have decreased in frequency and/or cover in our site A (Lovari et al. 2014; cf. Ferrari et al. 1988), suggesting a role of climatic changes in the reduction of pasture quality for chamois. Moreover, forb-dominated patches were more abundant in Site B than in Site A (Ferretti et al. 2015). Although our two sites were located at slightly different altitudes, the community composition of vegetation in the two sites is comparable, which would explain consistent responses of vegetation, bite rates and survival to weather dynamics across sites, during our study. In addition to weather variation, grazing by red deer principally reduces the availability of forage, whilst trampling increases the spatial fragmentation of vegetation cover; in fact, the volume of nutritious plants in the diet of female chamois declined faster, throughout summer-autumn, in areas grazed by deer than in the deer free site (Lovari et al. 2014; Ferretti et al. 2015). A potential for competition between red deer and chamois has been identified on several other mountainous systems (Schröder and Schröder 1984; Homolka and Heroldovà 2001; Bertolino et al.

2009; Redjadj et al. 2014; Anderwald et al. 2015, 2016). Direct and indirect factors (e.g., vegetation composition, intra-specific aggression, see below) may further affect bite rate and, potentially, kid survival, between sites. Nutritious pasture was more abundant in Site B than in Site A, and patches dominated by unpalatable plants were scarce in Site B, while covering a substantial proportion of grassland in Site A (Lovari et al. 2014; Ferretti et al. 2015; Corazza et al. 2016). Previous work has documented the spread of unpalatable, silica-rich, hairy grasses *Brachypodium genuense* in secondary meadows, i.e. our site A, as well as a greater abundance of spiny *Carduus carlinefolius* in that site (Lovari et al. 2014; Ferretti et al. 2015; Corazza et al. 2016). Patches with unpalatable plants are expected to limit further the availability of nutritious pasture and increase the spatial fragmentation of food patches, likely affecting foraging behaviour. Further work is needed to disentangle the role of different variables (including climate, grazing history and natural vegetation dynamics in secondary meadows) in determining observed vegetation composition of our study sites (Lovari et al. 2014; Ferretti et al. 2015; Corazza et al. 2016). In a depleted pasture, intraspecific competition is also expected to increase: if so, a greater level of social stress between individuals may occur, e.g. higher rates of aggression and/or vigilance (Sirot 2000). All of this emphasises why we would expect the bite rate to be lower in the deer-present site than in the deer-free one. Overall, the quantity and intensity of maternal care provided to offspring would be affected, decreasing the winter survival of chamois kids (Scornavacca et al. 2016). Current information suggests that weather changes, vegetation dynamics and interspecific competition are important limiting factors for Apennine chamois (Lovari et al. 2014; Ferretti et al. 2015; Corazza et al. 2016).

In vertebrates, early life conditions determine the fate of an individual (e.g. Lindström 1999; Lummaa and Clutton-Brock 2002). Food depletion and/or reduced access to high-quality forage during nursing/weaning will limit maternal investment; this can lead to short-term negative effects on offspring growth and survival (e.g. Festa-Bianchet and Jorgenson 1997; Therrien et al.

2008; Scornavacca et al. 2016), and/or long-term reductions in body size, phenotypic quality and reproductive success (Festa-Bianchet et al. 1994; Andres et al. 2013; Douhard et al. 2013). In turn, this can have a negative impact on population dynamics (Gaillard et al. 1998). Our estimated rate of decline in Site A (*c*. 50% in 35 years) is actually quite optimistic, as chamois numbers have decreased by *c*. 50% in 10-15 years (Lovari et al. 2014). Our results supported a negative effect of interspecific competition on the survival of chamois kids (Ferretti et al. 2015; present study). Our results suggest that summer drought conditions may also decrease kid survival (cf. Loison et al. 1999a), even in the absence of competition, although our dataset is based on only 4 years and our findings require confirmation. For example, winter and/or spring conditions may play a role in influencing vegetation dynamics and, consequently, growth/survival of offspring. Long-term population counts and time series for both spring-summer and winter climatic conditions (e.g. Forchhammer et al. 1998; Portier et al. 1998; Loison et al. 1999a; Kreylin et al. 2010), plus snow cover persistence in spring/early summer, would be useful to link population dynamics explicitly to climate and competition.

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Figure captions

Fig. 1 Foraging behaviour of adult female chamois, in summer, in an area grazed by red deer also (2010-2013; *n* = 357 sampling bouts): predicted bite rate *vs* rainfall in previous 45 days, in forb-dominated patches (left) and in graminoid-dominated patches (right). ●: 2010; ▲: 2011; ■ : 2012; +: 2013.

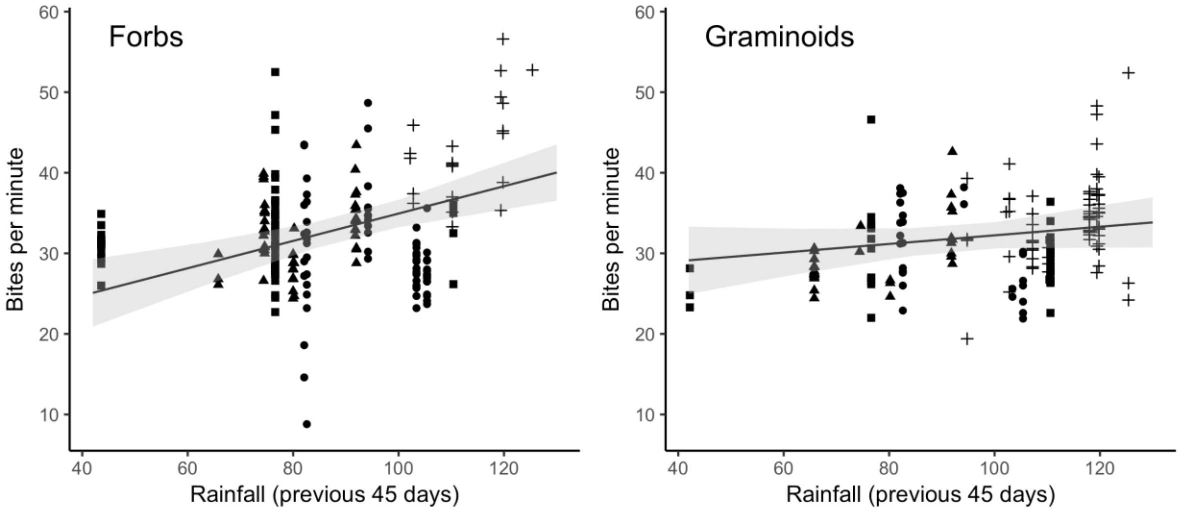
Fig. 2 Foraging behaviour of adult female chamois, in summer, in an area grazed by red deer also and in a deer-free area (2012-2013; *n* = 180 sampling bouts, Site A; *n* = 177, Site B): predicted bite rate *vs* mean temperature in previous 45 days (top panels), in the deer-present (Site A) and in the deer-free one (Site B); predicted bite rate *vs* total rainfall in previous 45 days (bottom panels) in the deer-present area (Site A) and in the deer-free one (Site B). ●: 2012; ▲: 2013.

Fig. 3 Foraging behaviour of adult female chamois, in summer, in an area grazed by red deer also (2012-2013; *n* = 180 sampling bouts, Site A; *n* = 177, Site B): predicted bite rate of adult female chamois *vs* mean temperature in previous 45 days (top panels) in forb-dominated patches and in graminoid-dominated ones; predicted bite rate *vs.* total rainfall in previous 45 days (bottom panels) in forb-dominated patches and in graminoid-dominated ones. ●: 2012; ▲: 2013.

Fig. 4 Index of winter survival of chamois kids in two study areas with/without red deer (site A: deer absent; site B: deer present), in 2010-2013. The Arrow indicates the year with drought early in summer.

Fig. 5 Relative likelihood distributions for survival rates of kids (red: Site A; orange: Site B) and population growth rates (λ, blue: Site A; mauve: Site B) of Apennine chamois in Site A (red deer present) and in Site B (red deer absent). The broken horizontal line indicates a population growth rate of λ = 1; kid survival rates that would lead to that population growth rate are shown by the broken vertical lines. Best estimates for kid survival and population growth are shown by the filled (Site A) and open (Site B) circles. The scale of the relative likelihood distributions has been adjusted for aesthetic reasons.

Fig. 1


Forbs
Graminoids
Bites per minute
Rainfall (previous 45 days)
10
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40
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60
40
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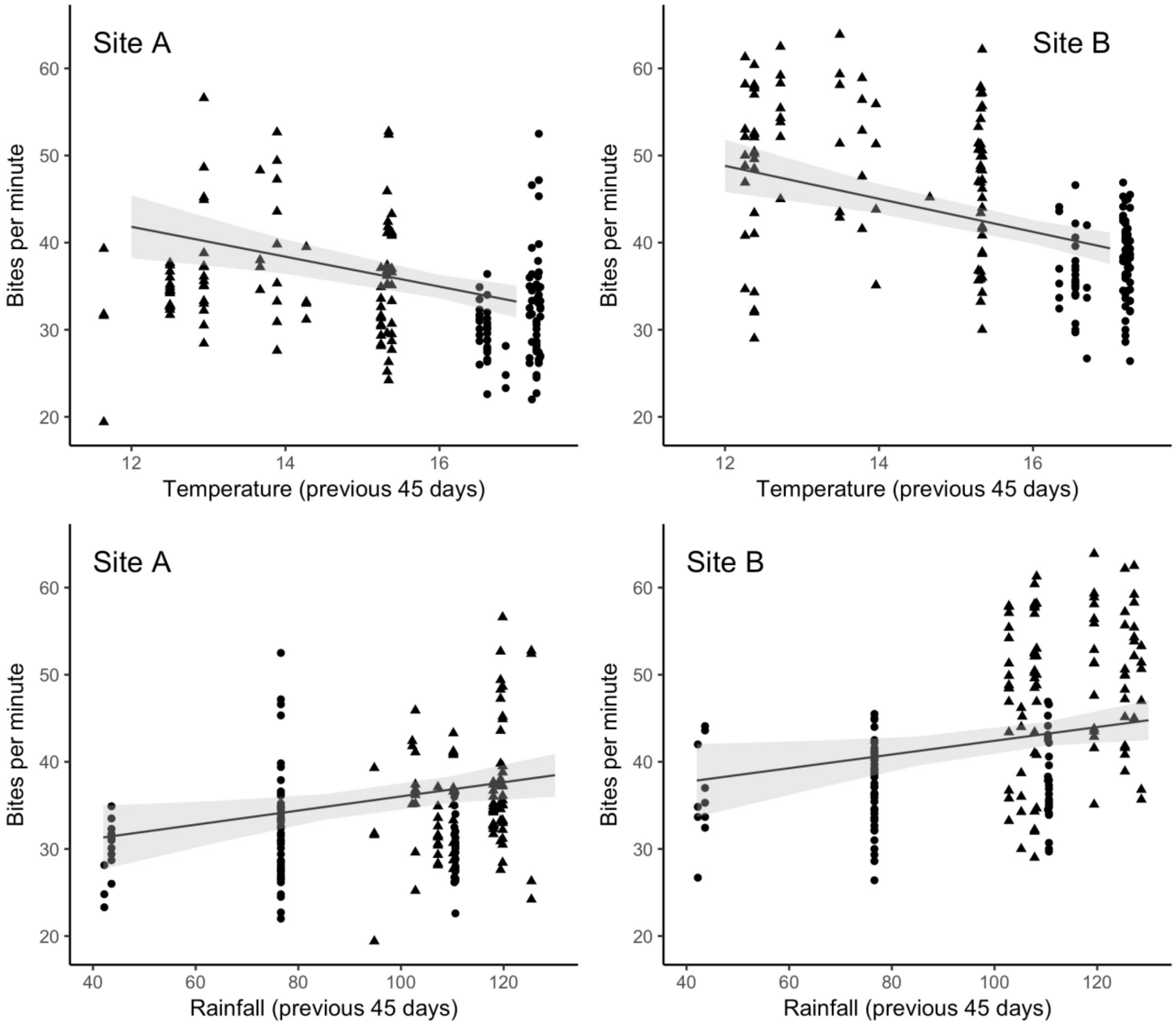
80
100
120

Fig. 2


Site A
Site B
Site A
Site B
Bites per minute
Bites per minute
Bites per minute
Bites per minute
20
30
40
50
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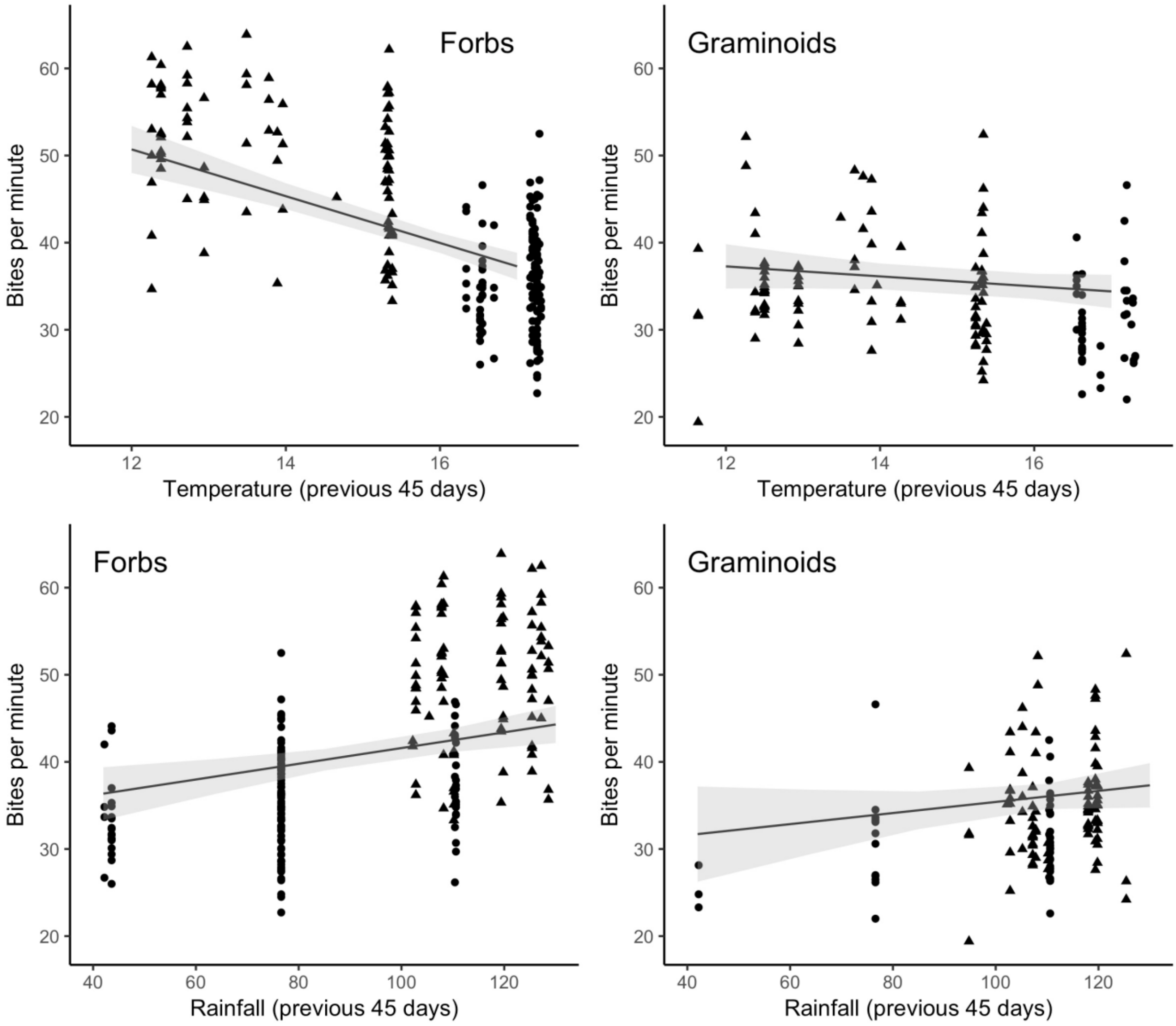
12
14
16
Temperature (previous 45 days)
Temperature (previous 45 days)
40
60
80
100
120
Rainfall (previous 45 days)
Rainfall (previous 45 days)

680 **Fig. 3**



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684 **Fig. 4**

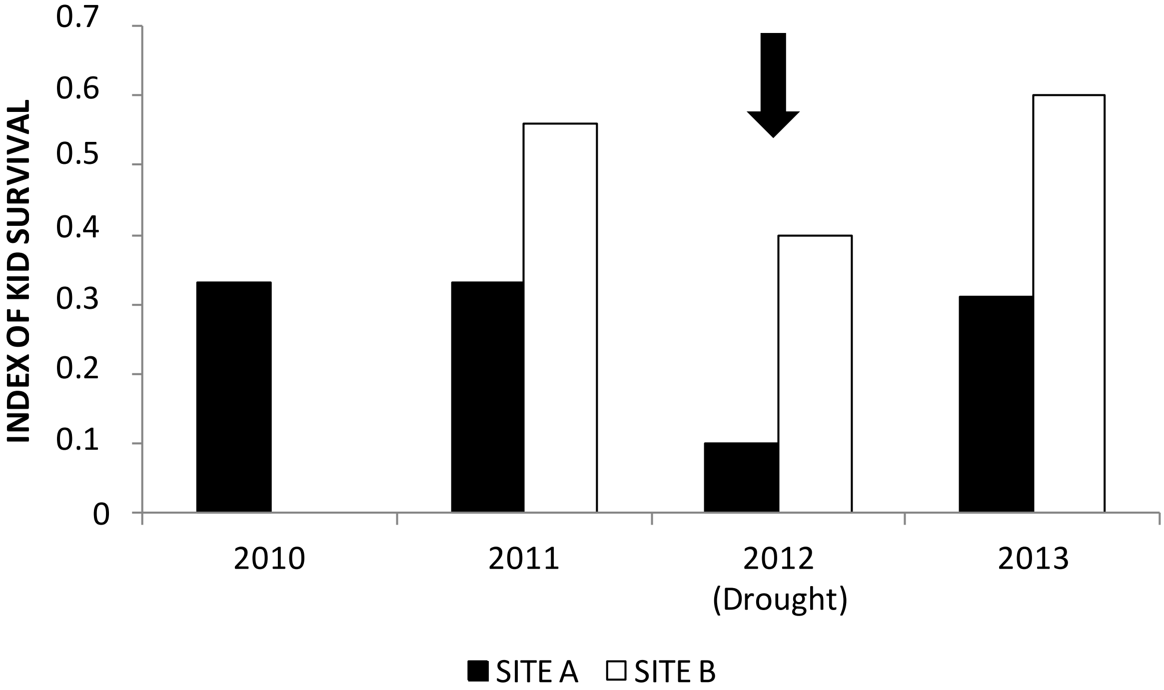
INDEX OF KID SURVIVAL
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
2010
2011
2012
(Drought)
2013
■ SITE A
□ SITE B

Fig. 5

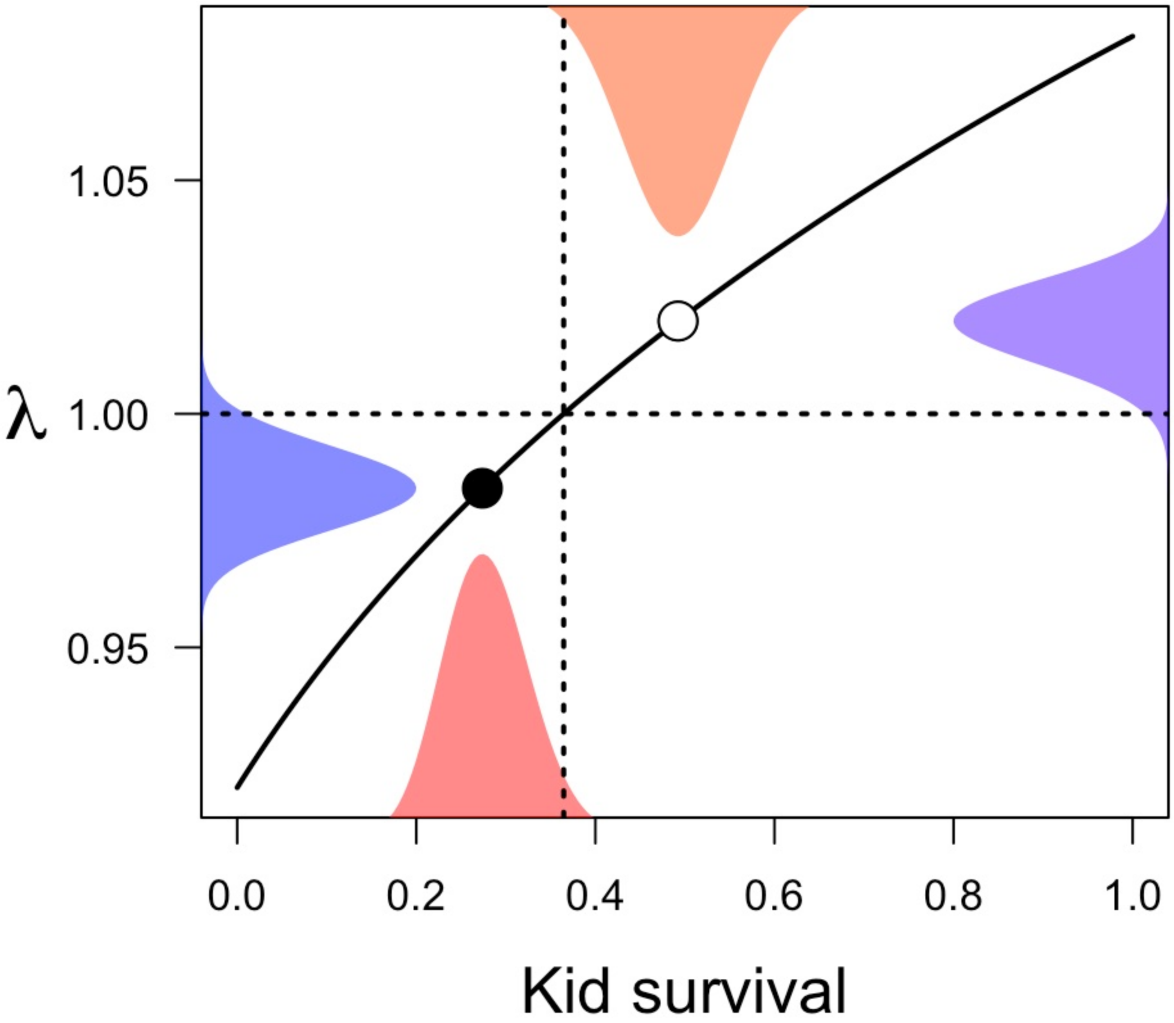

Table 1 List of predictors and random effects included in global models concerning variations of bite rate (1 site and 2 sites) and kid survival.

Model	Predictors	Random effects
Bite rate - 1 site	Mean temperature in previous days (45, 30 or 15)	Date
	Total rainfall in previous days (45, 30 or 15)	
	Time of day	
	Time of day^2	
	Vegetation type (forb-dominated; graminoid-dominated)	
	Extent of rock cover around the focal individual (0-25%; 25-50%; >50%)	
	Mean temperature × Vegetation	
	Total rainfall × Vegetation	
Bite rate - 2 sites	Mean temperature in previous days (45, 30 or 15)	Date
	Total rainfall in previous days (45, 30 or 15)	
	Site	
	Time of day	
	Time of day^2	
	Vegetation type (forb-dominated; graminoid-dominated)	
	Extent of rock cover around the focal individual (0-25%; 25-50%; >50%)	
	Mean temperature × Vegetation	
	Total rainfall × Vegetation	
	Mean temperature × Site	
	Total rainfall × Site	
Survival	Site	/
	Year	
	Site × Year	

Table 2 (a) Effects of weather on summer bite rate of adult female chamois, in the deer-present site, in 2010-2013 (*n* = 357 sampling bouts); (b) effects of weather on summer bite rate of adult female chamois, in two sites (Site A: red deer present; Site B: deer absent), in 2012-2013 (*n* = 180 sampling bouts, Site A; *n* = 177, Site B); (c) difference in winter survival of chamois kids between two study sites (Site A: red deer present; Site B: deer absent), throughout years (2011-2013). Summaries of selected models are shown, with AIC-best model in bold.

Model	**Variables retained**	**K**	**logLik**	**AICc**	**ΔAICc**	**Weight**
(a) Bite rate - 1 site	**Rain (45 days) + Veg + Rock cover + Time + Time^2 + Rain × Veg**	**10**	**-1072.449**	**2165.5**	**0.00**	**0.945**
	Temp (15 days) + Veg + Rock cover + Time + Time^2 + Temp × Veg	10	-1075.305	2171.2	5.70	0.055
(b) Bite rate - 2 sites	**Site + Temp (45 days) + Rain (45 days) + Veg + Rock cover + Time + Temp × Veg**	**11**	**-1093.510**	**2209.8**	**0.00**	**0.654**
	Site + Temp (45 days) + Rain (45 days) + Veg + Rock cover + Time.2 + Temp × Veg	11	-1094.150	2211.1	1.27	0.346
(c) Survival	**Site + Year**	**4**	**-76.157**	**160.6**	**0.00**	**0.625**
	Site	2	-78.787	161.7	1.03	0.375

Table 3 Estimated coefficients of variables influencing the bite rate of adult female chamois, in the deer-present site (a: 1 site models: $n = 357$ sampling bouts, 2010-2013) and in two sites (b: Site A: red deer present; Site B: deer absent, 2012-2013, $n = 180$ sampling bouts, Site A; $n = 177$, Site B). (c) difference in winter survival of chamois kids between two study sites (Site A: red deer present; Site B: deer absent), throughout years (2011-2013). Results of best models are shown.

Model Set	**Variables**	***B***	**s.e.**	**95% confidence intervals**	
(a) Bite rate - 1 site	Intercept	9.035	4.611	- 0.213	18.098
	Vegetation (Graminoids)	8.924	3.504	1.879	15.992
	Rock cover (>50%)	- 5.208	0.805	-6.781	-3.621
	Rock cover (25-50%)	- 1.595	0.591	- 2.758	- 0.431
	Time	1.751	0.477	0.813	2.690
	Time^2	- 0.067	0.020	-0.106	-0.027
	Rainfall (previous 45 days)	0.170	0.041	0.090	0.254
	Rainfall × Vegetation (Graminoids)	- 0.116	0.037	- 0.191	- 0.042
(b) Bite rate - 2 sites	Intercept	69.498	7.307	54.899	84.132
	Site (Deer absent)	6.541	0.776	4.990	8.057
	Vegetation (Graminoids)	- 38.754	5.805	- 50.199	- 27.344
	Rock cover (>50%)	- 3.627	0.787	- 5.214	- 2.056
	Rock cover (25-50%)	- 1.443	0.727	- 2.897	0.009
	Rainfall (previous 45 days)	0.084	0.022	0.037	0.132
	Temperature (previous 45 days)	- 2.684	0.366	- 3.418	- 1.952
	Time	0.309	0.086	0.141	0.477
	Temperature × Vegetation (Graminoids)	2.110	0.379	1.366	2.858
(c) Survival	Intercept	- 0.857	0.375	- 1.625	- 0.145
	Site (Deer absent)	1.237	0.409	0.455	2.066
	Year (2012)	- 0.914	0.450	- 1.819	- 0.047
	Year (2013)	0.051	0.516	- 0.969	1.066

Supplementary Material 1 Effects of weather on summer bite rate of adult female chamois, including date and temperature as linear predictors.

Supplementary Material 2 Estimated coefficients of variables influencing the bite rate of adult female chamois, including date and temperature as linear predictors.

Supplementary Material 3 Effects of weather on summer bite rate of adult female chamois, including date and temperature as linear predictors, including date but not temperature as linear predictor.

Supplementary Material 4 Estimated coefficients of variables influencing the bite rate of adult female chamois, including date but not temperature as linear predictor.

Supplementary Material 5 Cumulative rainfall and temperature, in summer, throughout the study period (2010-2013).

Supplementary Material 6 Model checking plots for bite rate models.