Multi-event capture-recapture analysis in Alpine chamois reveals contrasting responses to interspecific competition, within and between populations

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Abstract
1. Understanding components of interspecific competition has long been a major goal in ecological studies. Classical models of competition typically consider equal responses of all individuals to the density of competitors, however responses may differ both among individuals from the same population, and between populations.
2. Based on individual long-term monitoring of two chamois populations in sympathy with red deer, we built a multi-event capture-recapture model to assess how vital rates of the smaller chamois are affected by competition from the larger red deer.
3. In both populations, mortality and breeding probabilities of female chamois depend on age and in most cases, breeding status the preceding year. Successful breeders always performed better the next year, indicating that some females are of high quality. In one population where there was high spatial overlap between the two species, the survival of old female chamois that were successful breeders the preceding year (high-quality) was negatively related to an index of red deer population size suggesting that they tend to skip reproduction instead of jeopardizing their own survival when the number of competitors increases. The breeding probability of young breeders (ages 2 and 3) was similarly affected by red deer population size. In contrast, in the second site with low spatial overlap between the two species, the vital rates of female chamois were not related to red deer population size.
4. We provide evidence for population-specific responses to interspecific competition and more generally, for context-, age- and state-dependent effects of interspecific competition.
5. Our results also suggest that the classical assumption of equal responses of all individuals to interspecific competition should be relaxed, and emphasize the need to move towards more mechanistic approaches to better understand how natural populations respond to changes in their environment.

Keywords
Cervus elaphus, competitive interaction, demographic rates, individual quality, multi-event capture–mark–recapture, Rupicapra rupicapra
1 | INTRODUCTION

Species live in communities and when common limiting resources are shared among two species, interspecific competition can occur. Interspecific competition can ultimately lead to the exclusion of one of them, and cascading effects can change the composition of the entire community (Chesson, 2000; Kokkoris, Troumbis, & Lawton, 1999). Understanding components of interspecific competition has thus long been a major goal in ecological research across ecosystems (see Connell, 1983; Schoener, 1983 for reviews).

Nearly 100 years ago, the seminal work of Lotka (1925) and Volterra (1926) formulated the concept of interspecific competition mediated through shared and limited resources. They provided a well-known mathematical model of competition for finite resources in which the species-specific population growth rates depended on species-specific densities. This model is based on systems of differential equations where population sizes are state variables, and only focuses on population growth rates and competitive coefficients (Giacomini, DeAngelis, Trexler, & Petrere, 2013). It is by nature non-mechanistic, i.e. the specific competitive mechanisms are not explicitly stated or explored in the Lotka–Volterra model, assuming equal responses of all individuals to an increase in density of competitors.

Since then, applications and extensions of this model have flourished in the literature (McPeek, 2017; Terborgh, 2015). For instance, Gamelon et al. (2019) recently derived from the Lotka-Volterra’s competition model an approach where species-specific population growth rates depended on species- and age-specific densities. The authors applied this model to great tit Parus major and blue tit Cyanistes caeruleus, two competing species, and found that an increase in the density of the larger great tits resulted in a decrease of the population growth rate of the smaller blue tits. This pattern was observed at several sites across Europe and indicates a consistent marked negative effect of interspecific competition on blue tit’s population growth rate across all study sites.

Evidence is accumulating that sequential changes of demographic rates occur as population density of the focal species increases (i.e. intraspecific competition). In large mammals, it involves first a decrease in juvenile survival, followed by a decrease in reproductive rates of prime-aged females and finally a decrease in their survival (Bonenfant et al., 2009; Eberhardt, 1977, 2002; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000). Surprisingly, little is known on how population density of a competing species affects age-specific demographic rates of the focal species. However, to gain a good understanding on how an increase in density of a given competitor affects the population growth rate of the other species, it is crucial to identify whether individuals, according to their characteristics (e.g. age, reproductive state, from different populations), are differently affected in their demographic rates. Given the importance of individual heterogeneity in the dynamics of animal populations (Hamel et al., 2018), the time has come to challenge the assumption of equal responses of all individuals to an increase in density of competitors and to evaluate whether there are individual differences in responses to interspecific competition within a population (i.e. between individuals). Additionally, we need to explore whether the response to interspecific competition varies between populations. Exploring response to interspecific competition within and between populations will strengthen our understanding of competitive interactions under various environmental conditions.

Here, we take advantage of individual long-term monitoring of two Alpine chamois Rupicapra rupicapra populations living in sympatry with another ungulate species, the red deer Cervus elaphus. Previous works have shown that the diet of chamois and red deer shows considerable overlap in areas where they co-occur (Bertolino, Montezemolo, & Bassano, 2009; Lovari et al., 2014; Redjadj et al., 2014) and that the larger red deer might be a superior competitor over the smaller chamois (Anderwald, Haller, & Filli, 2016). In both chamois populations, females have been individually monitored for more than 20 years to determine their annual survival and reproduction. Simultaneously, an index of red deer population size has been recorded annually. Using a multi-event approach (Pradel, 2005), we investigate how the demographic performances of female chamois are related to the index of red deer population size. In particular, we identify whether, according to their characteristics (age/reproductive state, belonging to different populations), female chamois are differently affected in their demographic rates (survival and breeding probability) by an increase in red deer population size.

As Alpine environments are heterogenous habitats in terms of resource quality and quantity depending on altitude and on the exposure of the slopes (Nagy & Grabherr, 2009), we expect interactions between chamois and red deer to differ even at a small spatial scale and thus to differ between the two studied chamois populations (Anderwald et al., 2016). More specifically, previous works have shown that in one population, the low amount of high primary productivity (measured as Normalized Difference Vegetation Index) leads red deer to select meadows with high NDVI located at low altitudes during summer (Anderwald et al., 2016). At high altitudes, the limited amount of primary productivity is large enough to sustain chamois, more constrained by food quality than food quantity (Belovsky, 1986). This heterogeneity in the distribution of resources along the altitudinal gradient leads to strong segregation by elevation between the two species during summer. We thus expect no effect of red deer population size on chamois females in this first population. In contrast, in the other chamois population, red deer select meadows with high primary productivity and high solar radiation, coinciding with a positive selection for elevation, similar to the altitudinal selection by chamois (Anderwald et al., 2016; Herfindal, Anderwald, Filli, Campell Andrei, & Rempfler, 2019). In this site, there is little altitudinal segregation between the two species that occupy the same habitats in summer. We thus expect a significant effect of red deer population size on chamois females. Specifically, one can hypothesize that an increase in the red deer population size should affect the survival of the most vulnerable female chamois, such as senescent individuals. For females of other ages, we expect little effect of red deer, because the survival of long-lived species is known to be buffered against environmental variation (Gaillard & Yoccoz, 2003; Morris & Doak, 2004). However, in order not to jeopardize their survival when the number
of competitors increases, female chamois could skip reproduction. We thus expect a negative effect of red deer population size on the breeding probability of female chamois.

2 | MATERIALS AND METHODS

2.1 | Study sites

This study was conducted on two chamois populations within the Swiss National Park in the central Alps (46°40′N, 10°12′E). One population is located in the 5,026 ha area of Il Fuorn (first population, low spatial overlap between chamois and red deer during summer) and one in the 2,000 ha area of Val Trupchun (second population, high spatial overlap between the two species; see Figure 1). Both areas range between 1,800 and 2,800 m a.s.l. and are inhabited by two competing species, chamois and red deer. Hunting is not allowed in the National Park and the only predator is the Golden eagle *Aquila chrysaetos* that may attack kids. The two sites have markedly different environmental contexts. Previous studies have shown that exchange of individuals (red deer and chamois) between the two study areas is limited (Anderwald et al., 2016).

![Map of the two study sites (Val Trupchun with high spatial overlap between red deer and chamois; Il Fuorn with low spatial overlap) in the Swiss National Park. Displayed are the summer ranges (between June and September) for red deer (red) and chamois (blue; see also Anderwald et al., 2015, 2016; Herfindal et al., 2019) and population size index over years for both species.](image-url)
2.2 | Study species and data collection

Chamois females may reproduce for the first time at 2 years of age (Crampe et al., 2006; Morin, Rughetti, Rioux-Paquette, & Festa-Bianchet, 2016; Pioz et al., 2008; Figure 2). As births occur between May and June in the study areas, year was defined from 1 May in a given year to 30 April the next year (Figure 3). Between 1995 and 2016, 129 chamois females (87 at Il Fuorn and 42 in Val Trupchun) were captured all year-round using box or sling traps and marked with ear tags. The age at first capture, determined by counting growth rings on the horns (Schröder & von Elsner-Schack, 1985), ranged between 0 and 17 years old (see Appendix S1 for the distribution of age at first capture). Most females were captured as prime age, and only eight females at Il Fuorn and five females in Val Trupchun were captured as kids (i.e. in their first year of life). Ear-tagged females were monitored annually between June and October to assess their reproductive status. During that period, females observed at least once with a kid were considered as successful breeders. Females observed at least twice without kid were considered as failed breeders. For females seen only once without a kid or not detected at all between June and October (but observed in the periods May–June and/or October–May), we assumed that the reproductive status was unknown (see Appendix S2).

In parallel with individual monitoring, counts of red deer and chamois were performed annually at maximum seasonal densities, i.e. during July–August by experienced park rangers (Figure 3). Counts were performed in the same area within each study site for both species. Il Fuorn was divided into seven blocks and Val Trupchun into five blocks. Censuses were then conducted from the exact same points each year, selected for their optimal viewshed. Counts were performed for 2 weeks, chosen for their optimal viewing conditions (for further details, see Haller, 2006). Double counting of individuals at adjacent blocks was avoided by noting the time of the sightings, the exact location and the group composition and by sharing this information between rangers thanks to radio contact (Sæther et al., 2002). Thus, the invested effort in avoiding double counts and the open landscape suggest that counts are precise compared to most other ungulate

![Figure 2](image-url) Life cycle of the Alpine chamois. 1-year old females at $t$ may survive until $t+1$ with a probability $1-m_{0-1}$. Females in age class 2–12 at $t$ may survive until $t+1$ with a probability $1-m_{2-12}$. Senescent females (>12 years old) at $t$ may survive until $t+1$ with a probability $1-m_{>12}$. Females can start reproducing at age 2 with a breeding probability of $\psi_2$ and they reproduce with a probability $\psi_3$ at age 3. Females in age class 4–12 and senescent females have a breeding probability of $\psi_{4-12}$ and $\psi_{>12}$ respectively.

![Figure 3](image-url) Timeline showing the periods of capture–mark (all year-round), resighting of marked chamois (from July to October) and red deer population censuses (second half of July). For each period, the type of data collected is indicated. Capital letters correspond to months.
population counts (Sæther et al., 2002). The same protocol was applied twice during the 2-week counting period and a higher number of counted individuals was kept as a proxy of the minimum red deer (and chamois) population size index (Anderwald et al., 2015 for a similar approach; see also Anderwald et al., 2016; Herfindal et al., 2019). Population counts may have some weaknesses. First, annual variations in red deer population size index can be confounded with annual variations in detectability (Pollock et al., 2002). Note that here, both the location of the censuses (counting points) and the period to perform population counts have been carefully chosen for their optimal viewing conditions by experienced park rangers thus minimizing the risk of spurious correlation between population size index and detectability. Second, our population counts can lead to severe underestimates of the true population size but they provide reliable population indices to track temporal changes in red deer population size index (see Corlatti, Gugiatti, & Pedrotti, 2016 for a study in central Italian Alps).

2.3 | Capture–mark–recapture model

To estimate annual mortality, breeding and resighting probabilities, we used a multi-event approach (Pradel, 2005) implemented in E-SURGE (Choquet, Rouan, & Pradel, 2009). Chamois females at Il Fuorn and Val Trupchun are subjected to markedly different environmental contexts and are expected to exhibit contrasting demographic responses to an increase in the strength of interspecific competition, measured as an increase in the red deer index; therefore, we analysed the two chamois populations separately. There is currently no specific test to assess goodness-of-fit (GOF) of multi-event models (Pradel, 2005). Therefore, we ran the GOF test from the Cormack–Jolly–Seber (CJS) model using U-CARE (Choquet et al., 2009). For both sites, the global test was not statistically significant (Il Fuorn: $\chi^2 (56) = 67.00$, $p = 0.149$; Val Trupchun: $\chi^2 (38) = 29.21$, $p = 0.846$) indicating no lack of fit.

Females can be in three different states: (1) failed breeder (i.e. with no kid), (2) successful breeder (i.e. with one kid) or (3) dead (Figure 4). We dealt with state uncertainty by assessing the likelihood of a female state given the observation (i.e. event) in the field using a multi-event approach (Pradel, 2005). We considered four events for a female: (0) not detected; (1) detected as a failed breeder (i.e. observed at least twice with no kid between June and October); (2) detected as a successful breeder (i.e. observed at least once with a kid between June and October); (3) detected

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**FIGURE 4** Illustrative figure showing the between-state transition process (biological process) and the structure of the observation process (events). First, failed breeders (in green, FB) at year $t$ may survive until $t + 1$ with a probability $1 - m_{FB}$ or die with a probability $m_{FB}$. Successful breeders (in grey, SB) at year $t$ may survive until $t + 1$ with a probability $1 - m_{SB}$ or die with a probability $m_{SB}$. Second, failed breeders at year $t$ may remain failed breeders at year $t + 1$ with a probability $1 - \psi_{SB-SB}$ or become successful with a probability $\psi_{SB-SB}$. Successful breeders at year $t$ may remain successful at year $t + 1$ with a probability $1 - m_{SB}$ or fail with a probability $1 - \psi_{SB-SB}$. Four events (i.e. observations) are considered for a female: event 0—not detected; event 1—detected as a failed breeder; event 2—detected as a successful breeder; event 3—detected but reproductive status unknown. Failed breeders may not be detected with a probability $1 - p_{FB}$, detected as a failed breeder with a probability $p_{FB} \times (1 - \gamma_{FB})$, or detected with unknown reproductive status with a probability $p_{SB} \times (1 - \gamma_{SB})$. Successful breeders may not be detected with a probability $1 - p_{SB}$, detected as a successful breeder with a probability $p_{SB} \times \gamma_{SB}$ or detected with unknown reproductive status with a probability $p_{SB} \times (1 - \gamma_{SB})$. Dead females are not necessarily observed.
but reproductive status unknown (Figure 4). Females with no kid (state 1) may not be detected (event 0) with a probability $1 - p_{FB}$, detected as a failed breeder (event 1) with a probability $p_{FB} \times \gamma_{FB}$ (with $\gamma_{FB}$ the probability for assigning correctly the reproductive status for failed breeders) or detected with unknown reproductive status (event 3) with a probability $p_{SB} \times (1 - \gamma_{FB})$. Similarly, females with one kid (state 2) may not be detected (event 0) with a probability $1 - p_{SB}$, detected as a successful breeder (event 2) with a probability $p_{SB} \times \gamma_{SB}$ (with $\gamma_{SB}$ the probability for assigning correctly the reproductive status for successful breeders) or detected with unknown reproductive status (event 3) with a probability $p_{SB} \times (1 - \gamma_{SB})$ (Figure 4). Dead females (state 3) are necessarily not detected (event 0; Appendix S3). We assumed that resighting probability depends on female breeding status (i.e. failed or successful breeders; Figure 4).

From May at year $t$ to May at year $t+1$, females can die with a probability $m_{SB}$ for failed breeders and $m_{SB}$ for successful breeders (Figure 4; Appendix S4). For those who survive, failed breeders may become successful breeders with a probability $\psi_{SB-FB}$ and successful breeders may remain successful from 1 year to the next with a probability $\psi_{SB-SB}$ (Figure 4, Appendix S5). We tested whether mortality $m$ and/or breeding probabilities $\psi$ at year $t+1$ depended on (a) breeding status at year $t$ (i.e. $m_{SB} \neq m_{FB}$ and/or $\psi_{SB-SB} \neq \psi_{FB-SB}$); (b) age at year $t$; (c) red deer population size index at year $t$; we added the yearly population counts as a covariate on mortality $m$ and/or breeding probabilities $\psi$. We modelled age-specific mortality probabilities, we considered the three age classes previously described in these populations (see Bleu et al., 2015 for a description of these age classes in the study areas): age class 1, age class 2–12 and age class >12 (Figure 2). Because the age class 1 brings together few kids (captured at different ages in their first year of life, and most often after the peak of juvenile mortality) and females of age 1 (Figure 2), mortality $m_{SB}$ for this age class was likely underestimated. We thus focused on the age classes 2–12 and >12. For breeding probabilities, because reproduction is expected to be lower for 2 and 3 years old than for older females, we considered four age classes: age 2, age 3, age class 4–12 and age class >12 (Figure 2).

We tested different biologically meaningful models for the effects of breeding status at $t$, age and red deer population size index on breeding and mortality probabilities in the two chamois populations (see Appendix S6 for a list of all models tested). We used the Akaike’s information criterion (AIC; Burnham & Anderson, 2002) to select the best model. When AIC values were within two units, the most parsimonious model was retained. In addition, when red deer population size index was retained in the best models, we used an ANODEV to quantify the proportion of breeding/mortality probabilities for chamois explained by red deer population size index (Grosbois et al., 2008). The proportion of breeding/mortality probabilities for chamois explained by red deer population size index ($R^2$) was assessed by comparing deviance of models with the covariate on mortality $m$ and/or breeding probabilities $\psi$ ($\text{Dev}_{\text{dear}}$), to the constant ($\text{Dev}_{\text{const}}$) and the time-dependent models ($\text{Dev}_{t}$) (Skalski, Hoffmann & Smith 1993), such that:

$$R^2 = \frac{\text{Dev}_{\text{const}} - \text{Dev}_{\text{dear}}}{\text{Dev}_{\text{const}} - \text{Dev}_{t}}.$$

3 | RESULTS

3.1 | Population size index

Population counts indicate that chamois population size has fluctuated over the last 20 years in both sites, with index of maximum counts varying from about 270 to 650 individuals (mean = 488 [SE: 95]) at Il Fuorn (site with low overlap) and from around 90 to 220 individuals (mean = 159 [SE: 34.3]) in Val Trupchun (site with high overlap; Figure 1). Similarly, red deer population size has fluctuated from around 350 to 540 individuals (mean = 470 [SE: 55]) at Il Fuorn and between about 370 and 640 individuals (mean = 458 [SE: 65]) at Val Trupchun (Figure 1).

3.2 | No effect of interspecific competition on chamois survival

At Il Fuorn (site with low overlap), the most parsimonious model (model M1, Appendix S6) indicates that mortality is age-dependent, being the highest for senescents (>12 years of age; Figure 5). In addition, mortality probability between year $t$ and $t+1$ depended on breeding status at year $t$ (Figure 5). In particular, successful breeders at $t$ had lower mortality compared to failed breeders (i.e. $m_{SB} < m_{SB}$). For instance, successful breeders at $t$ had an annual mortality probability equals to 0.02 (SE: 0.01) at ages 2–12 and 0.13 (SE: 0.05) when older, whereas these probabilities were 0.10 (SE: 0.03) and 0.29 (SE: 0.04) for failed breeders. Red deer population size index had no effect on the mortality probability of successful breeders (M38, Appendix S6), failed breeders (M37, Appendix S6) or both successful and failed breeders (M36, Appendix S6).

In Val Trupchun (site with high overlap), the best model (model M40, Appendix S6) indicates that mortality is age-dependent, being higher for the oldest age class (Figure 6). Mortality probability were 0.09 (SE: 0.02) at ages 2–12 and 0.39 (SE: 0.08) for senescents (Figure 6). Red deer population size index had no effect on the mortality probability of successful breeders (M29, Appendix S6), failed breeders (M28, Appendix S6) or both successful and failed breeders (M27, Appendix S6). Thus, at Il Fuorn and Val Trupchun, chamois mortality probability was not influenced by interspecific competition from red deer, irrespective of the breeding status and age of the chamois.

3.3 | Effects of interspecific competition on chamois breeding probability are population-, age- and state-specific

At Il Fuorn, the site with low overlap, the best model indicates that breeding probability at $t + 1$ is strongly age-dependent, decreasing
from the age class 4–12 to the senescent class (>12 years of age; Figure 5). In addition, breeding probability at \( t + 1 \) depended on breeding status at year \( t \) (Figure 5), such that successful breeders at \( t \) were also the females that exhibited the highest breeding rates at \( t + 1 \) (i.e. \( \psi_{SB-SB} > \psi_{FB-SB} \)). The probability for successful breeders to breed the next year was 0.66 (SE: 0.04) at ages 4–12 and 0.38 (SE: 0.06) when older, whereas the breeding probability at \( t + 1 \) for failed breeders at \( t \) was 0.48 (SE: 0.06) at ages 4–12 and 0.17 (SE: 0.04) when older. For younger females, the breeding probability for females of 2 and 3 years old was estimated to be \( \psi_2 = 0.28 \) (SE: 0.14) and \( \psi_3 = 0.77 \) (SE: 0.11). There was no effect of red deer population size index on the breeding probability of females of any age or breeding status in II Fuorn (models M2, M3, M8, M9, Appendix S6). This indicates that at II Fuorn, red deer population size index did not affect breeding probability of the chamois.

In Val Trupchun where chamois spatially overlap with red deer, the best model indicates that breeding probability at \( t + 1 \) is also strongly age-specific (Figure 6) and depended on breeding status in year \( t \) (Figure 6). Successful breeders at \( t \) of ages 4–12 always had a higher probability to breed again at \( t + 1 \) (0.74 [SE: 0.06]) compared to failed breeders (0.26 [SE: 0.07]; Figure 6). For senescent females, failed breeders at \( t \) had a probability to breed at \( t + 1 \) estimated to be 0.41 (SE: 0.18). Noticeably, breeding probability at \( t + 1 \) for successful breeders at \( t \) depended on red deer population size index: the higher the red deer population size index, the lower the probability to breed again at \( t + 1 \). The analysis of deviance of this best model including red deer population size index as a covariate on breeding probability for females of >12 years of age (M40, Appendix S6, Dev\(_{\text{pred}}\) = 670.660), compared with the constant model (Dev\(_{\text{const}}\) = 675.280) and the time-dependent models (Dev\(_{\text{t}}\) = 658.122) revealed that red deer population size index explained 26.9% of the observed variance in
the breeding probability of successful breeders in the class >12 years old (i.e. $R^2 = 0.269$). Similarly, the breeding probability of females of age 2 and 3 depended on red deer population size index: chamois females simply did not reproduce from a given density of competitors (Figure 6). The analysis of deviance of the best model including red deer population size index as a covariate on breeding probability for females of age 2 (M40, Appendix S6, $Dev_{\text{deer}} = 670.660$), compared with the constant model ($Dev_{\text{const}} = 677.828$) and the time-dependent models ($Dev_t = 669.954$), revealed that red deer population size index explained 91.0% of the observed variance in the breeding probability of 2-year old females (i.e. $R^2 = 0.910$). For females of age 3, the analysis of deviance of the best model including red deer population size index as a covariate on breeding probability (M40, Appendix S6, $Dev_{\text{deer}} = 670.660$), compared with the constant model ($Dev_{\text{const}} = 673.888$) and the time-dependent models ($Dev_t = 666.616$), revealed that red deer population size index explained 44.4% of the observed variance in the breeding probability of 3-year old females (i.e. $R^2 = 0.444$). Thus, at Val Trupchun, red deer population size index had a negative effect on chamois breeding probability for females of age 2 and 3, and for senescent females that had already reproduced the previous year.

4 | DISCUSSION

Classical models of competition between two species such as Lotka (1925) and Volterra (1926) use linear combinations of two densities. These nonmechanistic models do not include the underlying demographic pathways through which interspecific competition operates. Here, we took advantage of unique individual long-term monitoring of two chamois populations in sympathy with red deer and used a multi-event capture-mark-recapture modelling approach to analyse how interspecific competition affects the demographic performances of female chamois. We showed that breeding probabilities of female chamois could be influenced by the presence of red deer competitors. These effects of red deer population size index on chamois differed between the two populations, the age and the reproductive status of the female, suggesting that the effect of interspecific competition on population dynamics operates through complex pathways.

In both populations, mortality and breeding probabilities of female chamois were age-dependent. Mortality increased from the prime-aged class (2–12 years old) to the oldest age class (females of age 13 and older), providing further evidence for actuarial senescence in wild populations (Loison, Festa-Bianchet, Gaillard, Jorgenson, & Jullien, 1999; Nussey, Froy, Lemaître, Gaillard, & Austad, 2013) and more specifically in this species (Bleu et al., 2015). Breeding probabilities for prime-aged females depended on their previous breeding status. Females that bred in the preceding year consistently had the highest breeding probabilities the following year (and the lowest mortality at Il Fuorn). These results clearly indicate that females that bred at year $t$ do not exhibit reduced survival and/or reproduction at year $t + 1$, contrary to the theory of reproductive trade-offs that predicts fecundity and/or survival costs at $t + 1$ for females that bred at $t$ (Bleu, Gamelon, & Saether, 2016; Roff, 2002; Williams, 1966). Instead, this positive covariation among demographic rates suggests marked individual heterogeneity in demography, with two types of females: high versus low quality individuals (Markussen et al., 2018; Tettamanti, Grignolino, Filli, Apollonio, & Bize, 2015; Weladji et al., 2008; Wilson & Nussey, 2010). High-quality females are consistently better in acquiring and allocating resources to both survival and reproduction (van Noordwijk & de Jong, 1986).

Regarding the effects of red deer population size index on chamois demographic rates, we provided evidence for population-specific responses to interspecific competition. At Il Fuorn (site with low overlap), red deer population size index had no effect on female chamois, in accordance with results from an earlier study in this site (Anderwald et al., 2016), which could not detect any effect of interspecific competition on horn growth in young, a proxy of body condition. Spatial heterogeneity in the distribution of resources may allow chamois to rely on food resources at higher altitudes than red deer (Anderwald et al., 2015, 2016), decreasing the spatial overlap between the two species and thus the potential for competitive interactions. In Val Trupchun where the spatial overlap between red deer and chamois is higher, breeding probability at $t + 1$ of senescent successful breeders at $t$ was reduced at high red deer population size index, and red deer population size index explained 26.9% of the observed variance in breeding probability. This indicates that when red deer population size increases, old high-quality females tend to skip reproduction instead of jeopardizing their own survival, a pattern classically observed in long-lived species (Gaillard & Yoccoz, 2003). We found the same demographic response to increasing red deer population size for young females of age 2 and 3, i.e. an increased propensity to skip reproduction with increasing density of competitors. Accordingly, previous study at Val Trupchun found reduced horn growth in young chamois when red deer population size increases (Anderwald et al., 2015), providing additional evidence for interspecific competition in this area. High red deer population size can explain the marked effect of interspecific competition on chamois. In addition, in Val Trupchun, red deer rely on food resources located at high altitudes, which coincide with the area occupied by chamois, preventing spatial segregation between the two species and increasing interspecific competition for resources.

Our findings clearly show that the effects of interspecific competition are context-, age- and state-dependent and that demographic rates are differently affected by interspecific competition. Although interspecific competition explains a large proportion of the variance in some demographic rates (e.g. up to 91% of the breeding probability of 2-year old females), the remaining part of the variance still may be due to multiple environmental factors such as weather conditions or habitat quality. Comparative studies have revealed strong influence of weather conditions on many demographic traits in cervids (Saether, 1997). For instance, snow cover a given year and its resulting effect on the duration of the
The growing season of the vegetation may have negative long-lasting effects on chamois survival (Jonas, Geiger, & Jenny, 2008; Loison, Jullien, & Menaut, 1999; Willisch et al., 2013). The effects of harsh environmental conditions can also be age-dependent, and typically the young and senescent individuals are more sensitive to poor weather conditions (see e.g. Loison, Jullien, et al., 1999, on chamois; Coulson et al., 2001, on Soay sheep Ovis aries; Hansen et al., 2019, on reindeer Rangifer tarandus). In contrast, according to the demographic buffering hypothesis (Hilde et al., 2020; Morris & Doak, 2004), survival of the prime-aged class (2–12 years old) that has the highest impact on population growth rate of long-lived species is expected to be partly canalized/buffered against environmental changes (Gaillard & Yoccoz, 2003) through an adjustment of the reproductive effort (Festa-Bianchet, Côté, Hamel, & Pelletier, 2019). As we found a negative effect of interspecific competition on old and young ages and not on survival of prime-aged females, it is likely that the impact of red deer population size on chamois population growth rate is limited. Assessing the overall impact of interspecific competition on chamois population dynamics remains to be carefully explored. An exciting perspective to achieve such a goal could be to combine capture–mark–recapture (CMR) data on chamois with population counts within the framework of an integrated population model (Zipkin & Saunders, 2018).

There is accumulating evidence that natural populations are influenced by the combined effects of environmental factors and intra-specific density dependence (Boyce et al., 2006; Coulson et al., 2001; Leirs et al., 1997), chamois making no exception (Willisch et al., 2013). Interestingly, at Il Fuorn (site with low overlap), red deer and chamois population sizes exhibited similar temporal variation (Pearson's correlation coefficient = 0.570; \( p = 0.007 \)) and similar average population sizes (Figure 1). As we did not find any effect of red deer population size index on chamois demographic rates in this site, we can hypothesize that neither interspecific nor intraspecific density dependence play a key role in shaping chamois demographic rates. At Val Trupchun (site with high overlap), red deer were on average three times more abundant than chamois and population sizes exhibit different temporal variation for both species (Pearson's correlation coefficient = 0.151; \( p = 0.514 \)). Thus, the observed decrease of breeding performances for young and senescent chamois with increasing red deer population size index seemed not to be confounded by possible intraspecific density-dependent responses. However, a definite answer would require accurate estimates of population size for both chamois and red deer, which remains challenging with unmarked individuals.

Species do not live in isolation but live in community with other species that can rely on common limiting resources. Therefore, to gain a comprehensive picture of the dynamic of a focal population, it is crucial to account for species interactions. A growing body of empirical and theoretical evidence shows that CMR data are powerful to reach such a goal. For instance, by analysing jointly CMR data and population counts, Pérön and Koons (2012) developed a Bayesian multi-population integrated model to assess the competitive interactions of two sympatric duck species. Here, we show that multi-event capture-recapture models can be powerful tools to understand how a competing species influences the demographic performances of a sympatric species. While we focused on pairwise interactions, demographic rates of chamois could also be influenced by other competitors, as for example ibex present at Val Trupchun (Herfindal et al., 2019). Expanding our approach to more than two species offers promising avenues of research (Levine, Bascompte, Adler, & Allesina, 2017).

We provide evidence for contrasting demographic responses to an increase in the density of competitors, the responses to interspecific competition being age-, state-, context- and rate-specific. We thus strongly recommend relaxing the assumption of equal responses of all individuals to interspecific competition and to move towards more mechanistic approaches. Mechanistic models are crucial to better understand how natural populations respond to changes in their environment and will ultimately help us to predict their dynamics in a changing world (Urban et al., 2016).

ACKNOWLEDGEMENTS
We warmly thank Rémi Choquet, Guillaume Souchay, Anne Loison, Jean-Michel Gaillard and one anonymous reviewer for helpful comments on an earlier version of this manuscript. We also thank Stefano Focardi for stimulating discussions about ungulate monitoring. We thank the Swiss National Park for collecting and managing data with the help of many volunteers. This work was supported by the Research Council of Norway (SFF-III 223257 and project number 244647).

AUTHORS' CONTRIBUTIONS
M.G. and I.H. developed the concept and idea; F.F. contributed to the data collection; I.H. prepared the datasets; M.G. conducted the analyses and wrote the manuscript with input from all authors.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.c866t1g49 (Gamelon, Filli, Saether, & Herfindal, 2020).

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REFERENCES
Anderwald, P., Haller, R. M., & Filli, F. (2016). Heterogeneity in primary productivity influences competitive interactions between red deer and Alpine chamois. PLoS ONE, 11, e0146458. https://doi.org/10.1371/journal.pone.0146458
Anderwald, P., Herfindal, I., Haller, R. M., Risch, A. C., Schütz, M., Schweiger, A. K., & Filli, F. (2015). Influence of migratory ungulate management on competitive interactions with resident species in a protected area. Ecosphere, 6, art228. https://doi.org/10.1890/ES15-00365.1
Belovsky, G. E. (1986). Generalist herbivore foraging and its role in competitive interactions. Integrative and Comparative Biology, 26, 51–69. https://doi.org/10.1093/icb/26.1.51
between reintroduced red deer and Apennine chamois. Animal Conservation, 17, 359–370. https://doi.org/10.1111/acv.12103
Markussen, S. S., Loison, A., Herfindal, I., Solberg, E. J., Haanes, H., Reed, K. H., ... Sæther, B.-E. (2018). Fitness correlates of age at primiparity in a hunted moose population. Oecologia, 186, 447–458. https://doi.org/10.1007/s00442-017-4021-2
McPeek, M. A. (2017). Evolutionary community ecology. Princeton, NJ: Princeton University Press.
Morin, A., Rughetti, M., Rioux-Paquette, S., & Festa-Bianchet, M. (2016). Older conservatives: Reproduction in female Alpine chamois (Rupicapra rupicapra). Animal Conservation, 17, 359–370. https://doi.org/10.1111/acv.12103
Roff, D. A. (2002). Life history evolution. Sunderland, MA: Sinauer Associates Inc.
Saether, B.-E. (1997). Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. Trends in Ecology & Evolution, 12, 143–149. https://doi.org/10.1016/S0169-5347(96)10068-9
Saether, B.-E., Engen, S., Filli, F., Aanes, R., Schröder, W., & Andersen, R. (2002). Stochastic population dynamics of an introduced swiss population of the ibex. Ecology, 83, 3457–3465. https://doi.org/10.1890/3072094
Schoener, T. W. (1983). Field experiments on interspecific competition. The American Naturalist, 122, 240–285. https://doi.org/10.1086/284133
Schröder, W., & von Elsner-Schack, I. (1985). Correct age determination in chamois. In S. Lovari (Ed.), The biology and management of mountain ungulates (pp. 65–70). London, UK: Croom Helm
Skalski, J. R., Hoffmann, A., & Smith, S. G. (1993). Testing the significance of individual- and cohort-level covariates in animal survival studies. In J. D. Lebreton & P. M. North (Eds.), Marked individuals in the study of bird populations (pp. 9–28). Basel, Switzerland: Birkhauser Verlag.
Terborgh, J. W. (2015). Toward a trophic theory of species diversity. Proceedings of the National Academy of Sciences of the United States of America, 112, 11415–11422. https://doi.org/10.1073/pnas.1501071112
Tettamanti, F., Grignolio, S., Filli, F., Apollonio, M., & Bize, P. (2015). Senescence in breeding success of female Alpine chamois (Rupicapra rupicapra): The role of female quality and age. Oecologia, 178, 187–195. https://doi.org/10.1007/s00442-014-3197-y
Urban, M. C., Bochedi, G., Hendry, A. P., Mihoub, J.-B., Peer, G., Singer, A., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. Science, 353(6304), aad8466. https://doi.org/10.1126/science.aad8466
van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. The American Naturalist, 128, 137–142. https://doi.org/10.1086/284547
Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. Nature, 118, 558.
Weladji, R. B., Loison, A., Gaillard, J.-M., Holand, Ø., Mysterud, A., Yoccoz, N. G., ... Stenseth, N. C. (2008). Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia, 156, 237–247. https://doi.org/10.1007/s00442-008-0961-x
Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack’s principle. The American Naturalist, 100, 687–690. https://doi.org/10.1086/282461
Willisch, C. S., Bieri, K., Struch, M., Franceschina, R., Schnidrig-Petrig, R., & Ingold, P. (2013). Climate effects on demographic parameters in an un hunted population of Alpine chamois (Rupicapra rupicapra). Journal of Mammalogy, 94, 173–182. https://doi.org/10.1644/10-mamm-a-278.1
Wilson, A. J., & Nussey, D. H. (2010). What is individual quality? An evolutionary perspective. Trends in Ecology & Evolution, 25, 207–214. https://doi.org/10.1016/j.tree.2009.10.002
Zipkin, E. F., & Saunders, S. P. (2018). Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation, 217, 240–250. https://doi.org/10.1016/j.biocon.2017.10.017

SUPPORTING INFORMATION
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How to cite this article: Gamelon M, Filli F, Saether B-E, Herfindal I. Multi-event capture-recapture analysis in Alpine chamois reveals contrasting responses to interspecific competition, within and between populations. J Anim Ecol. 2020;89:2279–2289. https://doi.org/10.1111/1365-2656.13299