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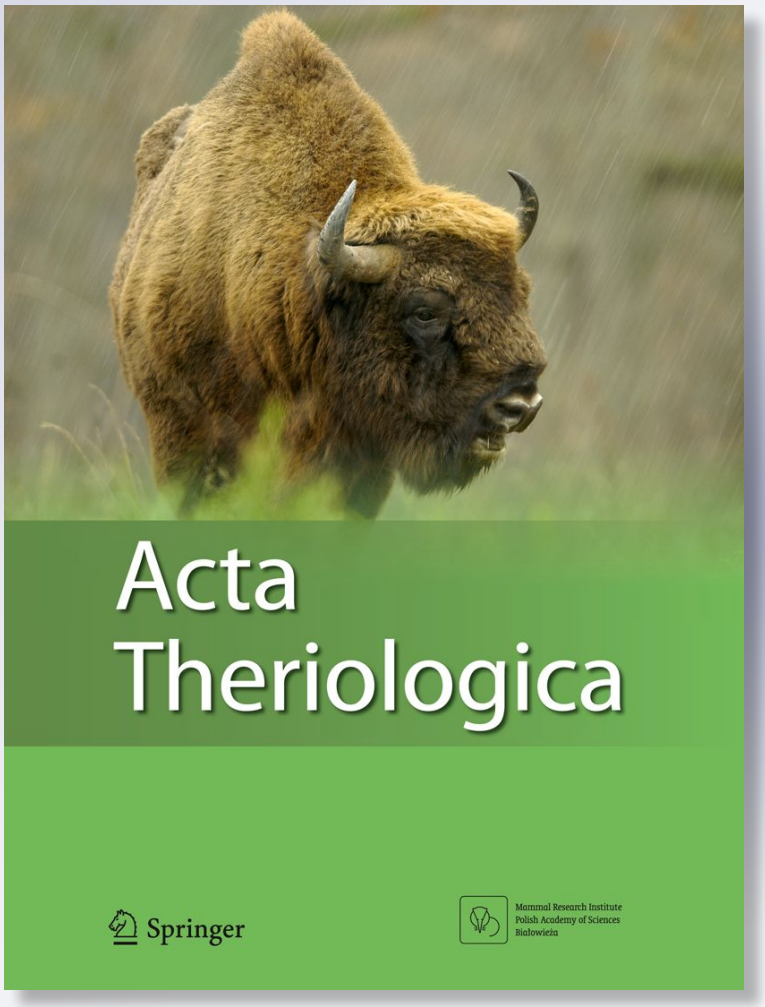

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ORIGINAL PAPER

Effects of an exceptionally snowy winter on chamois survival

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Abstract Although weather-induced mass mortalities of wild ungulates have been reported, no study has quantified how these episodes may affect the survival of prime-aged adults. Long-term studies of marked ungulates have instead consistently found very weak or no effects of weather on the survival of this age class, particularly for females. We report on the effects of the exceptionally snowy winter of 2008–2009 on three populations of chamois in the western Alps: two in Italy, one in France. In the Alpi Marittime Natural Park in Italy, mortality of prime-aged females (aged 2–9 years) was 43%, about five times higher than reported by previous studies of chamois. Just across the continental divide in the adjacent Mercantour National Park (PNM) in France, however, prime-aged female mortality was only 6%. Senescent females suffered very high mortality in both populations (100% and 56%). In the Gran Paradiso National Park in Italy and in the Alpi Marittime Natural Park, adult male mortality rate was respectively of 81% and 44%, whereas in the PNM, it was only 10%. A recent reduction in population density in the French population, or lower absolute snowfall than in Italy, may explain the difference in survival. Survival of males and prime-aged females can be affected by exceptional weather events, possibly in combination with high population density. Adult chamois of both sexes appeared to show elevated mortality in response to harsh winter conditions. Our results underline the importance of considering sex and age classes in evaluating the impacts of population density in wild ungulates.

Keywords *Rupicapra rupicapra* · Age structure · Weather · Winter mortality · Snow fall

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Introduction

Large mammals are strongly iteroparous and typically produce small litters. Consequently, longevity is the main determinant of female lifetime reproductive success in these species (Bérubé et al. 1999; Festa-Bianchet et al. 2003; Beauplet et al. 2006; Pistorius et al. 2008). Females appear selected to prioritize their own survival when allocating energy to maintenance and reproduction, because the survival of juveniles is much lower and more variable than that of adult females (Gaillard et al. 2000; Beauplet et al. 2006). In ungulates, survival of prime-aged females is typically 90–95% and varies little from year to year (Gaillard et al. 1998; Gaillard et al. 2000). In most species,

prime-aged females are between 2 and 7–9 years of age (Gaillard et al. 2000). Typically, the survival of juveniles and of senescent individuals is more susceptible to various sources of mortality than that of prime-aged females, which is mostly density independent and not affected by weather (Gaillard et al. 1998; Gordon et al. 2004) regardless of species, habitat type, ecosystem type or variability in the major source of mortality (Gaillard et al. 2000).

The survival of prime-aged female ungulates has very high elasticity, so that its decline would have a drastic impact on the rate of population growth (Gaillard et al. 2000; Coulson et al. 2005). Consequently, factors that affect the survival of prime-aged females play an important role on ungulate population dynamics. In dimorphic and polygynous ungulates, males have higher energy requirements than females due to their larger body size. Males adopt riskier reproductive tactics than females, to achieve high dominance rank and increase reproductive success (Gaillard et al. 2000). Consequently, males should be less capable than females to buffer yearly variation in environmental conditions. For chamois (*Rupicapra rupicapra*), however, there appears to be very little sexual difference in adult survival, despite moderate size dimorphism and possibly strong polygyny (Loison et al. 1999; Bocci et al. 2010).

Most reports of drastic declines in ungulate population are associated with disease, predation or hunting. Exotic diseases, transmitted from livestock (Loison et al. 1996; Cransac et al. 1997; Jorgenson et al. 1997) and predator-pit situations, particularly for small populations (Owen-Smith et al. 2005; Wittmer et al. 2005; Festa-Bianchet et al. 2006) can increase adult female mortality, depressing population growth. Although harsh weather is often thought to increase mortality in all age classes, we have been unable to find any reports of severe weather specifically affecting the survival of prime-aged female ungulates. Some catastrophic declines in large herbivore populations probably involved high mortality of prime-aged females (moose, *Alces alces* (Peterson 1999), caribou, *Rangifer tarandus pearyi* (Tews et al. 2007) and red kangaroo, *Macropus rufus* (Caughley and Gunn 1993)), but none of these studies quantified age-specific mortality because the age structure of animals at risk of mortality was unknown. Long-term studies of marked, known-age ungulates generally report little or no effects of weather on prime-age survival of either sex (Gaillard et al. 1998).

In the western Alps, the winter 2008–2009 was characterized by exceptional snowfall. We examined its consequences for the survival of adult (2–9 years old) and senescent (10 years and older) chamois in three populations. We expected that the harsh winter would substantially lower the survival of senescent but not of prime-aged females and that males would not suffer much higher mortality than females, as previously reported for this species (Loison et al. 1999; Bocci et al. 2010).

Material and methods

Study areas

We monitored marked, known-aged chamois in three parks in the western Alps: the Alpi Marittime Natural Park (PNAM) in southern Piedmont, Italy (44° N, 7° E), the adjacent Mercantour National Park (PNM) in France (44° N, 7° E) and the Gran Paradiso National Park (PNGP) in northern Piedmont (45° N, 7° E). In most years, snow cover at 1,500 m elevation lasts from December to April in all three areas. The topography is rugged, including rocks and moraines that are dominant in the Italian parks (47% PNAM, 59% PNGP and 10% PNM). Pastures cover about 60% of PNM. Forests, dominated by beech (*Fagus sylvatica*) at low elevation, are replaced by mixed forest of conifers (*Larix deciduas* and *Picea abies*) as altitude increases. Shrub and alpine pastures cover vegetated areas above the tree line. There is no legal chamois hunting in any of the three areas.

Weather data

Weather data were obtained from meteorological stations located within each study area. The time span during which data were collected and the indexes used to assess winter harshness varied across stations. Therefore, we could not directly compare snowfall amounts in the different areas. Instead, we compared snowfall among years in each study area.

In the Alpi Marittime Natural Park, 490 cm of snow fell during winter 2008–2009 (November 1 to April 30), 66% greater than the long-term average of 295 cm and the fourth highest since records began in 1927. Snow cover at 1,500 m lasted from early December 2008 to early June 2009. The average monthly snow depth in PNM for the three snowiest months was 165 cm in winter 2008–2009, more than twice the average of 78 cm in the previous 10 years. Snow cover lasted longer than usual, with an April snow depth of 153 cm compared to an average of 47 cm over the ten previous years. In GPNP, average snow depth during winter 2008–2009 (November 1 to May 31) was 227 cm, almost twice the average of 115 cm over the last 47 years and more than three times the average of 68 cm for the previous 10 years.

Population data and statistical analysis

Sex- and age-class-specific mortality was estimated for the winter 2008–2009, based on individually marked chamois. In PNAM and PNGP, chamois were captured in spring with a dart gun. Adult females in PNAM received very high frequency (VHF) radio collars, other chamois were marked with ear tags and visual collars. In PNGP, only males were

captured. Animals were subsequently monitored weekly by ground observations and radiotracking. In PNAM, monitoring effort was greater in April–May and October–November, to document parturition and kid survival to weaning. Chamois were considered dead when carcasses, collars or tags were recovered. Because all radio-collared females alive during a given year were resighted at least once in each of the previous April–May and October–November periods, we assumed that those not seen from April to November 2009 had died. None of the females assumed to be dead was sighted during fieldwork in 2010. In PNAM between April and November 2009, marked males were seen twice on average (range one to five times). For PNAM and PNGP, we assumed that males that were not seen in either 2009 or 2010 had died. In PNM, chamois were captured with cage traps or drop nets baited with salt. All captured chamois were equipped with VHF collars with mortality sensors and signals were checked three to seven times a week. In all three areas, age was estimated at capture from horn increments (Schroder and Elsner-Schack 1985).

Winter survival was estimated according to sex, age class and study area as the proportion of surviving individuals. Bayesian 95% credible intervals for these estimates were calculated using WinBUGS 1.4.3. (Lunn et al. 2000) as the 7.5th and 97.5th percentiles of 100,000 samples drawn by Markov Chain Monte Carlo from a binomial posterior distribution assuming an uninformative prior (McCarthy 2007).

Results

In PNAM, we recovered radio collars or ear tags for 12 dead females during summer 2009. An additional seven marked females were not observed from April to November and were considered dead. Of 30 females aged 2–9 years, 13 died (43% mortality). All six females aged 10 years and older died (Table 1). Of 11 marked males aged 2–9 years alive in October 2008, 7 survived to April 2009, for a mortality rate of 36%. Three of seven males aged 10 years and older survived to April 2009 (57% mortality).

In PNM, only 2 of 34 females aged 2–9 years died (6% mortality), but just 4 of 9 females, 10 years and older, survived to April (56% mortality, Table 1). Of the 30 radio-collared males aged 2–9 years alive in October 2008, 3 died during winter (10% mortality).

In the PNGP, of 16 marked adult males alive in October 2008, only 3 were known to survive in the winter for a catastrophic mortality of 81% (Table 1). Of the missing 13 males, 7 were recovered dead and 7 were not seen despite intensive searches of the study area in 2009 and 2010. Marked males in the Gran Paradiso were mostly senescent with 15, aged 9 years or older. The only male, aged 4 years, survived.

Discussion

We documented an exceptional mortality of prime-aged female chamois in the PNAM, likely caused directly by the abundant snowfall. The very high mortality for females older than 10 years both in PNAM and PNM supports suggestions that senescent ungulates are more sensitive than prime-aged ones to weather conditions (Gaillard et al. 2000; Gordon et al. 2004). All previous studies of marked known-age female ungulates found very high survival, typically 90–95% (Gaillard et al. 1998) and independent of winter severity or adverse spring weather (Klein and Olson 1960; Barrett 1982; Loison and Langvatn 1998). During a severe winter, mortality of prime-aged female chamois in PNAM was seven times higher than the 6% reported by previous

Table 1 Sex- and age-specific survival of chamois in Alpi Marittime Natural Park in Southern Piedmont (PNAM), Italy, the adjacent Mercantour National Park (PNM) in France and the Gran Paradiso National Park (PNGP) in Northern Piedmont

Study area	Sex	Age (years)	Number alive autumn 2008	Number alive spring 2009	Survival rate	95% Credible intervals
PNAM	Females	2–9	30	17	0.57	0.39–0.73
		≥10	6	0	0.00	0.00–0.41
	Males	2–9	11	7	0.63	0.35–0.84
		≥10	7	3	0.43	0.16–0.76
PNM	Females	2–9	34	32	0.94	0.81–0.98
		≥10	9	4	0.44	0.19–0.74
	Males	2–9	30	27	0.90	0.74–0.96
PNGP	Males	≥9[a]	16	3	0.19	0.07–0.43

Details on the calculation of 95% credible intervals are provided in the text

[a] One male, among the survivors, was 4 years old, all others were aged at least 9 years

studies of this species and of Pyrenean chamois (*Rupicapra pirenaica*) (Loison et al. 1994, 1999; Gonzales and Crampe 2001). In the adjacent PNM, however, the mortality of prime-aged females remained at 6%, despite an exceptional amount of snow. That difference between adjacent populations could be due to the combined effects of weather and density. The PNM population had declined drastically the previous year because of an epizootic of keratoconjunctivitis (C. Toïgo, unpublished data), possibly leaving a low-density population with high resource availability. On the other hand, the recorded amount of snowfall in PNM, although higher than usual, appeared lower than that recorded in PNAM, and was possibly insufficient to strongly affect the survival of adult chamois. Nevertheless, the contrasting results confirm the overall pattern that survival of prime-aged female ungulates is only exceptionally affected by weather (Gaillard et al. 1998).

The survival of adult males was much lower in the PNAM than in the PNM, confirming the pattern seen for females, with "normal" mortality in PNM and high mortality in PNAM. The very low survival of PNGP males was likely partly due to their advanced age, but it was much lower than the 75–80% survival reported for old male Pyrenean chamois (Loison et al. 1999). Overall, sex- and age-specific survival data for PNAM and PNM confirm earlier reports that adult chamois mortality does not differ substantially according to sex (Loison et al. 1999; Bocci et al. 2010).

Our results underline the importance of considering sex and age classes in evaluating the impacts of change in survival on population growth of wild ungulates (Festa-Bianchet et al. 2003). Senescent females suffered high mortality independently of study area, but the high mortality of prime-aged females in PNAM led to a marked decline in population density.

Mortality patterns in PNAM suggest that the winter 2008–2009 presented chamois with an exceptional challenge. Even though mountain ungulates are adapted to harsh winters, occasional catastrophic events can affect adult survival, population size and population dynamics. The Alpine ibex (*Capra ibex*) population in the PNGP is strongly affected by weather, with severe declines when winters with exceptional snow depth are combined with high population density (Jacobson et al. 2004). In ibex, snowfall may act mostly through an increase in the mortality of older individuals (Largo 2008). Alpine ibex populations can include many senescent individuals because survival from 1 to 9 years of age is very high for both sexes (Toïgo et al. 2007).

Because of their rarity, it is difficult to include extreme weather events in management plans. Extreme climatic events are increasing in frequency and magnitude as a consequence of global climate change (Walther et al. 2002), affecting population growth of many species (Bolger et al. 2005; Thibault and Brown 2008). Stochastic perturbations can have a strong impact on the population dynamics of wild ungulates. Global climate change may require a greater consideration of the effects of extreme and unexpected climate events for conservation and management.

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