**Shrinking Alpine chamois: climate warming has led to a 3kg decrease in yearling body mass over 27 years in Southern Switzerland**

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**Abstract**

Climate change has been hypothesised to be partly driving the change in size observed in numerous species. We investigated the body mass changes of 5635 yearling Alpine chamois (*Rupicapra rupicapra*) harvested in September at 1.5 years of age in the Swiss Alps (Ticino canton) in relation to temperature from 1992 to 2018. Yearling chamois shrank by 2.97kg while temperatures between May and July raised by 1.7°C. Warmer temperatures were associated with lower mass of yearlings, with two periods having the strongest impact: birth and early lactation (May 9 to July 2) and, to a lesser extent, the summer (May 2 to July 21) previous to the harvest. The analysis of year-detrended mass and temperature data strongly supports the hypothesis that the increases in temperature during growth are responsible for the decrease in body mass of yearling chamois. Altogether, our results suggest that the rising temperatures in the Alpine regions could have significant consequences on the ecology and evolution of this wild ungulate.

Although climate change is considered to be partly responsible for the size change observed in numerous species, the relevance of this hypothesis for the Alpine chamois remains debated. Using body mass measurements of 5635 yearling (i.e. 1.5 years old) Alpine chamois (*Rupicapra rupicapra*) harvested in September in the Swiss Alps (Ticino canton) from 1992 to 2018, we first show that, during this period, yearlings shrank by 2.97kg while temperatures between May and July raised by 1.7°C. We identified that warmer temperatures during birth and early lactation (May 9 to July 2 in the year of birth), and to a lower extent during the summer (May 2 to July 21) they were harvested, had the strongest impact on yearling mass. Further analyses of year-detrended mass and temperature data strongly supports the hypothesis that the increases in temperature during growth are responsible for the decrease in body mass of yearling chamois. Altogether, our results suggest that the rising temperatures in the Alpine regions could have significant consequences on the ecology and evolution of this wild ungulate.

**Introduction**

As global changes induced by human activities accelerate, many species are undergoing phenotypic changes to adapt to their new environment [1], often measured by changes in distribution, abundance, and phenology. An increasingly reported response to climate warming is the change in animal body size and shape [2–4] as morphology affects thermoregulation [5]. Indeed, a shrinking in body size leads to a larger surface-area-to-volume ratio which, in turn, allows animals to dissipate heat more efficiently in warmer environments (Bergman rule; [6]). Global warming is also likely to have an impact on body size due to changes in food availability and quality [7]. Heat dissipation and nutrition are likely driving the phenotypic responses observed in free-living animals jointly [2]. This might be especially true in mammals where ambient temperature and the ability to dissipate heat have been demonstrated to constrain maternal milk production and offspring growth [5,8].

In vertebrates with finite growth (such as mammals and birds), the size an individual reaches as an adult has critical consequences for reproductive success and overall fitness [9]. As the adult size and mass are primarily determined by early growth conditions and juvenile size (e.g., [10]), it becomes fundamental to investigate early-life effects of climatic conditions [11]. Juveniles usually have low energy reserves and must allocate much of it to growth [12,13], making them sensitive to changing external biotic and abiotic factors [14–16]. In mammals, early growth is divided into three phases: gestation, lactation, and post-weaning. The three phases are, however, not equally sensitive to climate warming. Gestation is likely the less sensitive as offspring live in a stable thermal environment. In contrast, the lactation phase is likely the most sensitive, as offspring growth in size is the fastest during lactation and mother milk production is constrained by ambient temperature [5,8]

Here, we investigated the effect of climate change on changes in yearling size (i.e., 1.5 years of age) of Alpine chamois (*Rupicapra rupicapra*) using hunting data collected in the southern Swiss Alps from 1992 to 2018. The Alpine chamois is the most abundant ungulate of the European Alps [17], and its morphology and physiology are adapted to high-altitude (cold) environmental conditions [18]. Accordingly, most previous studies on the Alpine chamois have revealed a gradual shrinking in chamois body mass both in adults ([16], data from Italy and our study area) and in yearlings ([21,22], Italy and Austria). A recent study, however, did not find any change body mass or size in chamois and three other ungulate species in the eastern Alps [23], study region adjacent to ours. Although studies reporting a change in chamois body size have generally identified the critical period as the spring-summer temperatures over the first two years of life [16], no study has tried to precisely identify which time window during early-life is most sensitive to climate warming and whether the shrinking in body size over time is associated with an increase in temperature during this critical time window.

**Methods**

*Study system*

The Alpine chamois is an ungulate that shows early appearances of sexual dimorphism, with females reaching asymptotic body mass three years earlier (3.5 years) than males (6.2 years) [24–26]. In the Alps, chamois give birth in May [27], and the period from May to July corresponds to the lactation of kids in their first year of life and the growth peak of yearlings in their second year of life. Chamois are weaned between 3 and 6 months of age [28]. Vegetation in the Alps usually begins growing right after snowmelt in April, peaking in July, thus providing an abundant and protein-rich food source for a relatively brief period of time [29]. Alpine chamois are distributed over a broad altitudinal range (500–3100 m; [30,31]) and can shift their range depending on the resource availability and climate conditions [22,32].

Data on the size of chamois were collected in the southern Alps of Switzerland (canton Ticino) and consist of records of the hunting bags from 1992 to 2018. The study area covers an area of 2700 km2 with an altitude varying from 250 to 2700 m asl. In Ticino, hunting starts at the beginning of September and the harvest plan is mainly completed within three weeks. All animals were sexed, aged and weighed (eviscerated). Hunters estimated age by counting the growth rings of their horns [33]. Overall, 34017 animals were harvested during the hunting period (age range: 0.5-22.5 years old). We analysed yearling data (1.5-year-old, 5635 individuals, 2491 females and 3144 males) to cover this species fastest period of growth [26]. By September, yearlings have been feeding on their own for nearly a year, but they are still vulnerable to external threats due to the decrease in maternal care and increased active grazing behaviour.

Daily mean ambient temperature (℃) from 1990 until 2018 (all the years needed for the analysis) was obtained from a Swiss meteorological station in the city of Lugano (273 m asl), within the harvesting area. Other stations at higher elevation inside the study area had uncomplete data, but present high correlation values with the station of Lugano (all Pearson r > 0.8).

*Statistical analysis*

As the use of arbitrary climate periods does not always explain the biological response in the best way possible [34], we investigated the variation in yearling body mass in relation to the variation in mean ambient temperature using the package *climwin* [36] in R v4.2.1 [35]. This package allows the detection of the exact time window when a biological variable is most strongly affected by an environmental variable. Further details on the analysis are provided in the electronic supplementary material 1.

The overall approach for the *climwin* analysis is to compare the support of the data for competing hypotheses and to formalise them into regression models [34]. Competing models are based upon a baseline model (not including weather effects) and ranked using the ΔAICc (difference in terms of the Akaike Information Criterion values calculated for a small sample size between the baseline model and the model of interest). Our baseline model was a linear model with the body mass of the yearling chamois in relation to sex and elevation. The function *slidingwin* creates a set of competing models testing windows of different lengths for the weather variable of interest (here, mean daily ambient temperature). Non-linear effects of temperature on body mass were investigated by testing for linear and quadratic trends. As parameters in *slidingwin*, we set an absolute time window with September 24(last date of harvest) as reference day. We looked for windows between the reference dayand 661 days before (December 1 of two years before) to include the critical periods in a young chamois life: gestation, lactation, first winter and yearling. When the first window was found, we included it in the baseline model and re-run a *slidingwin* analysis to look for additional windows affecting body mass independently to our first window. Finally, we ran year-detrended analyses to demonstrate that year is not confounding the relationship between body mass and temperature [37]. We extracted the residuals of linear regressions between mass and year and between temperature and year, and then ran a linear model with the residuals of body mass in relation to the residuals of temperature.

**Results**

The final model included an effect of the sex of the individual, elevation and a quadratic effect of mean temperature between days 503 and 449 and between 145 and 65 from the reference day (September 24; Table 1 and Supplementary Materials 1). These climate windows are independent (Pearson’s correlation: *r* = 0.24, *t* = 1.24, df = 25, *P* = 0.23) and equivalent to the period from May 9 until July 2 of the birth year and to May 2 until July 21 of the harvest year. Most importantly, chamois body mass was lower with a higher average ambient temperature in both climatic windows (Table 1, Fig. 1a,b). Yearling chamois were heavier when harvested at higher elevations (Table 1, Fig. 1c), and males were heavier than females (mean ± SE mass in kilogram of males: 14.2 ± 0.05; females: 13.6 ± 0.06; Table 1).

Over the course of the study, the mean temperature between May 2 and July 21 (which encompasses our two climatic windows) increased by 0.06 °C per year (± 0.02 °C, *t* = 2.9, *P* = 0.007; Fig. 2a), leading to a 1.7°C increase in 27 years. On the other hand, the mean body mass of 1.5-year-old chamois decreased by 0.112 kg per year (± 0.006 kg, *t* = -17.81, *P* < 0.001; Fig. 2b), leading to an overall decrease in average mass of 2.92 kg during the years of the study. The analysis of year-detrended data showed a significant positive association between yearling body mass and the quadratic mean temperatures between May 2 and July 21 (*F* = 37.72, P < 0.001; Fig. 2c).

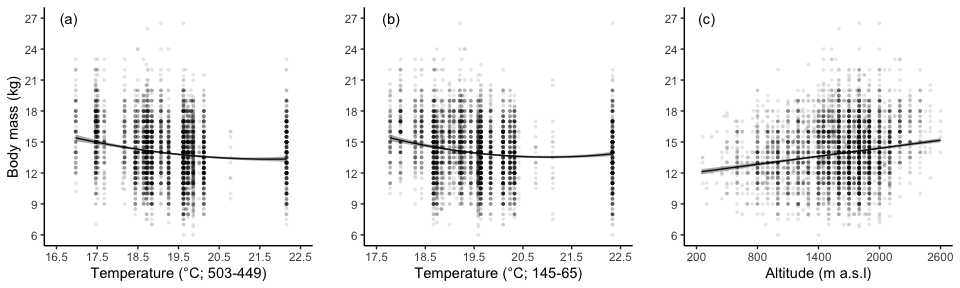
**Table 1**

Results of the linear model showing the quadratic effect of annual average temperature (°C) between May 9 and July 2 of the birth year (window: 503-449) and between May 2 and July 21 of the harvest year (window: 145-65), harvest elevation (m a.s.l.), and sex (Males vs Females) on body mass (kg) of harvested 1.5-year-old Alpine chamois. No. of observations: 5635 in 27 years.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Predictors* | *Estimate* | *SE* | *t* | *P* |
| Intercept | 11.867 | 0.153 | 77.78 | **<0.001** |
| T (window: 503-449) | -31.948 | 2.581 | -12.38 | **<0.001** |
| T (window: 503-449) ^2 | 14.294 | 3.262 | 4.38 | **<0.001** |
| T (window: 145-65) | -22.150 | 3.090 | -7.17 | **<0.001** |
| T (window: 145-65) ^2 | 21.821 | 2.787 | 7.83 | **<0.001** |
| Harvest elevation | 0.001 | 0.000 | 14.31 | **<0.001** |
| Sex [M] | 0.496 | 0.069 | 7.19 | **<0.001** |

**Figure 1**

Relationship between body mass of harvested 1.5-year-old Alpine chamois and (a) the average temperature between May 9 and July 2 of the birth year (lactation period), and the average temperature between May 2 and July 21 of their second year of life (harvest year), and (c) elevation (m a.s.l.). Each dot is one observation (darker dots represent a higher number of observations); fitted lines in (a) and (b) are shown with 95 % confidence intervals (shaded areas).



**Figure 2**

Annual trend of (a) average temperature between May 2 and July 21 and (b) body mass of harvested 1.5-year-old Alpine chamois between 1992 and 2018, and (c) year-detrended relationship between body mass and temperature. Detrended values in (c) are residuals from linear models in (a) and (b). Each dot is one observation (darker dots representing a higher number of observations in (b)); fitted lines are shown with 95% confidence intervals (shaded areas).

Chart

Description automatically generated

**Discussion**

Here we showed a marked decrease in body mass of yearling chamois in relationship to an increase temperature during a critical time for their growth. Our results indicated a decrease in body mass of almost 3kg and an increase in the average ambient temperature of ca. 1.7°C between late spring and early summer during this 27-year study (1992-2018), supporting previous research in this population [16,21,22]. We identified two crucial temperature windows during chamois development that were during spring and summer in their first year of life (around end of gestation and beginning of lactation), and during spring and summer in their second year of life (resuming of growth as yearling). Our study supports the hypothesis that spring-summer temperatures are more important than winter temperatures regarding phenotypic changes in seasonal environments [11,38], but make a further step by revealing times critical for chamois growth.

Climate change can affect chamois growth in several ways. First, chamois births no longer coincide with the highest peak of vegetation growth as a result of rising temperatures shifting the phenology of the plants they feed upon [39]. The lack of resources for mothers during the lactation period might influence how much energy might be allocated into nursing, with cascading effects on kid growth. However, this hypothesis is unlikely since annual birth peaks of herbivores are mainly influenced by day length, not by the resource availability [40]. Second, ambient temperatures can strongly influence the nutrient intake of yearling chamois during growth both by altering the feeding activity [21] of young and adults. During warm days, chamois have been shown to reduce heat-generating activities (including foraging), likely in an attempt to avoid thermal overload [7]. Third, climatic conditions may affect the body reserves of mothers, which in turn can affect the offspring growth during gestation [41] and lactation. Ambient temperatures can also directly affect the quantity and quality of milk production [42], with increasing temperatures leading to lower milk yield in domesticated ungulates [43,44]. Climate change can also affect milk composition, with a significant decline in milk protein and fat content in response to warmer temperatures [45,46].

Overall our results support previous studies stating the importance of climatic conditions for growing ungulates at high elevations and latitudes [14,16,22]. Animals can try to avoid heat stress by shifting their range to higher elevations [7] and latitudes, or by eating during the night [47]. Several large ungulate species have already become progressively more abundant at higher elevations in the past 30 years [48]. Accordingly, our results show that yearling chamois who were harvested at higher elevations, and thus, colder environments, have heavier body mass than the ones living at lower elevations (see also XX). These findings suggest that ungulates are expressing such changes in their behaviours and phenotype to cope with warming spring and summer temperatures. Yet, it remains to be understood whether size changes in response to summer temperatures may be detrimental to surviving the harsh wintering conditions at high elevations. Research is also needed on the long-term consequences of the changes in early growth on the whole life history of Alpine ungulates, from age at first reproduction to the onset of senescence and death, in order to adequately model the demographic consequences of climate change on these species.

~~Our results show a phenotypic change in a wild ungulate population that could lead to changes in life-history traits with significant consequences for the species population dynamics. Body size is a fundamental determinant of individual survival and reproduction (e.g., [50–53]) and the warming climate could therefore act as a selective pressure with long-term effects [54]. Further studies should monitor populations using long-term projects with marked individuals [55] to better investigate the ecological and evolutionary consequences of body size change in ungulates.~~

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**Data accessibility**

All data and code used for statistical analysis and plots are provided via the Open Science Framework at “link for OSF project”

**Authors' contributions**

G.M. and P.B. conceived the study. F.T. compiled the data and L.F.B and N.I curated the data. G.M. and K.G.G performed the statistical analyses with the help of P.B. G.M. and K.G.G drafted the manuscript and all authors provided inputs at all stages. All authors approved the final version of this manuscript, and all authors agree to be held accountable for the work performed therein.

**Competing interests**

We declare we have no competing interests.

**References**

1. Hetem RS, Fuller A, Maloney SK, Mitchell D. 2014 Responses of large mammals to climate change. *Temperature* **1**, 115–127. (doi:10.4161/temp.29651)

2. Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. 2011 Declining body size: A third universal response to warming? *Trends in Ecology and Evolution*. **26**, 285–291. (doi:10.1016/j.tree.2011.03.005)

3. Sheridan JA, Bickford D. 2011 Shrinking body size as an ecological response to climate change. *Nature Climate Change* **1**, 401–406. (doi:10.1038/nclimate1259)

4. Ryding S, Klaassen M, Tattersall GJ, Gardner JL, Symonds MRE. 2021 Shape-shifting: changing animal morphologies as a response to climatic warming. *Trends in Ecology & Evolution* **36**, 1036–1048. (doi:10.1016/j.tree.2021.07.006)

5. Speakman JR, Król E. 2010 Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms: Heat dissipation limit theory. *Journal of Animal Ecology* **79**, 726–746. (doi:10.1111/j.1365-2656.2010.01689.x)

6. Bergmann C. 1847 Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Abgedruckt aus den Göttinger Studien* **3**, 595–708.

7. Brivio F, Bertolucci C, Tettamanti F, Filli F, Apollonio M, Grignolio S. 2016 The weather dictates the rhythms: Alpine chamois activity is well adapted to ecological conditions. *Behav Ecol Sociobiol* **70**, 1291–1304. (doi:10.1007/s00265-016-2137-8)

8. Simons MJP, Reimert I, van der Vinne V, Hambly C, Vaanholt LM, Speakman JR, Gerkema MP. 2011 Ambient temperature shapes reproductive output during pregnancy and lactation in the common vole (Microtus arvalis): a test of the heat dissipation limit theory. *Journal of Experimental Biology* **214**, 38–49. (doi:10.1242/jeb.044230)

9. Beauplet G, Guinet C. 2007 Phenotypic determinants of individual fitness in female fur seals: larger is better. *Proceedings of the Royal Society B: Biological Sciences* **274**, 1877–1883. (doi:10.1098/rspb.2007.0454)

10. Festa-Bianchet M, Jorgenson JT, Réale D. 2000 Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology* **11**, 633–639. (doi:10.1093/beheco/11.6.633)

11. Garel M, Gaillard J-M, Jullien J-M, Dubray D, Maillard D, Loison A. 2011 Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *Journal of Mammalogy* **92**, 1112–1117. (doi:10.1644/10-MAMM-A-056.1)

12. Hudson RJ, White RG, editors. 1985 *Bioenergetics of wild herbivores*. Boca Raton, Fla: CRC Press.

13. Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C. 2000 Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. *Annual Review of Ecology and Systematics* **31**, 367–393.

14. Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD. 2001 Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**, 721–729. (doi:10.1046/j.0021-8790.2001.00532.x)

15. Herfindal I, Solberg EJ, Sæther B-E, Høgda KA, Andersen R. 2006 Environmental phenology and geographical gradients in moose body mass. *Oecologia* **150**, 213–224. (doi:10.1007/s00442-006-0519-8)

16. Rughetti M, Festa-Bianchet M. 2012 Effects of spring-summer temperature on body mass of chamois. *Journal of Mammalogy* **93**, 1301–1307. (doi:10.1644/11-MAMM-A-402.1)

17. Corlatti L, Lorenzini R, Lovari S. 2011 The conservation of the chamois Rupicapra spp. *Mammal Review* **41**, 163–174. (doi:10.1111/j.1365-2907.2011.00187.x)

18. Ascenzi P *et al.* 1993 Functional, spectroscopic and structural properties of haemoglobin from chamois (Rupicapra rupicapra) and steinbock (Capra hircus ibex). *Biochemical Journal* **296**, 361–365. (doi:10.1042/bj2960361)

19. Ernakovich JG, Hopping KA, Berdanier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD. 2014 Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology* **20**, 3256–3269. (doi:10.1111/gcb.12568)

20. Turco M, Palazzi E, von Hardenberg J, Provenzale A. 2015 Observed climate change hotspots. *Geophysical Research Letters* **42**, 3521–3528. (doi:10.1002/2015GL063891)

21. Mason TH, Apollonio M, Chirichella R, Willis SG, Stephens PA. 2014 Environmental change and long-term body mass declines in an alpine mammal. *Frontiers in Zoology* **11**, 69. (doi:10.1186/s12983-014-0069-6)

22. Reiner R, Zedrosser A, Zeiler H, Hackländer K, Corlatti L. 2021 Forests buffer the climate-induced decline of body mass in a mountain herbivore. *Global Change Biology* **27**, 3741–3752. (doi:10.1111/gcb.15711)

23. Büntgen U, Jenny H, Galván JD, Piermattei A, Krusic PJ, Bollmann K. 2020 Stable body size of Alpine ungulates. *Royal Society Open Science* **7**, 200196. (doi:10.1098/rsos.200196)

24. von Hardenberg A, Bassano B, Peracino A, Lovari S. 2000 Male Alpine Chamois Occupy Territories at Hotspots Before the Mating Season. *Ethology* **106**, 617–630. (doi:10.1046/j.1439-0310.2000.00579.x)

25. Bassano B, Perrone A, Hardenberg AV. 2003 Body weight and horn development im Alpine chamois, Rupicapra rupicapra (Bovidae, Caprinae). **67**, 65–74. (doi:10.1515/mamm.2003.67.1.65)

26. Garel M, Loison A, Jullien J-M, Dubray D, Maillard D, Gaillard J-M. 2009 Sex-Specific Growth in Alpine Chamois. *Journal of Mammalogy* **90**, 954–960. (doi:10.1644/08-MAMM-A-287.1)

27. Rughetti M, Festa-Bianchet M. 2011 Effects of early horn growth on reproduction and hunting mortality in female chamois. *Journal of Animal Ecology* **80**, 438–447. (doi:10.1111/j.1365-2656.2010.01773.x)

28. Scornavacca D, Cotza A, Lovari S, Ferretti F. 2018 Suckling behaviour and allonursing in the Apennine chamois. *Ethology Ecology & Evolution* **30**, 385–398. (doi:10.1080/03949370.2017.1423115)

29. Pettorelli N, Pelletier F, Hardenberg A von, Festa-Bianchet M, Côté SD. 2007 Early Onset of Vegetation Growth Vs. Rapid Green-up: Impacts on Juvenile Mountain Ungulates. *Ecology* **88**, 381–390. (doi:10.1890/06-0875)

30. Shackleton DM. 1997 Wild sheep and goats and their relatives : status survey and conservation action plan for Caprinae.

31. Spitzenberger F, Bauer K, Mayer A, Weis E, Preleuthner M, Sackl P, Sieber J. 2001 *Die Säugetierfauna Österreichs*. Bundesministerium für Land-und Forstwirtschaft, Umwelt und Wasserwirtschaft.

32. Nesti I, Posillico M, Lovari S. 2010 Ranging behaviour and habitat selection of Alpine chamois. *Ethology Ecology & Evolution* **22**, 215–231. (doi:10.1080/03949370.2010.502316)

33. Schroder W, Elsner-Schack IV. 1985 Correct age determination in chamois. In *The biology and management of mountain ungulates*, pp. 65–70. London, United Kingdom: Croom Helm.

34. van de Pol M, Bailey LD, McLean N, Rijsdijk L, Lawson CR, Brouwer L. 2016 Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution* **7**, 1246–1257. (doi:10.1111/2041-210X.12590)

35. R Core Team. 2022 R: A language and environment for statistical computing. R Foundation for Statistical Computing.

36. Bailey LD, van de Pol M. 2016 climwin: An R Toolbox for Climate Window Analysis. *PLoS ONE* **11**, e0167980. (doi:10.1371/journal.pone.0167980)

37. Iler AM, Inouye DW, Schmidt NM, Høye TT. 2017 Detrending phenological time series improves climate–phenology analyses and reveals evidence of plasticity. *Ecology* **98**, 647–655. (doi:10.1002/ecy.1690)

38. Klein DR. 1965 Ecology of Deer Range in Alaska. *Ecological Monographs* **35**, 259–284. (doi:10.2307/1942139)

39. Chirichella R, Stephens PA, Mason THE, Apollonio M. 2021 Contrasting Effects of Climate Change on Alpine Chamois. *The Journal of Wildlife Management* **85**, 109–120. (doi:10.1002/jwmg.21962)

40. Post E, Forchhammer MC. 2008 Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 2369–2375. (doi:10.1098/rstb.2007.2207)

41. Hansen PJ. 2009 Effects of heat stress on mammalian reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 3341–3350. (doi:10.1098/rstb.2009.0131)

42. Liu J, Li L, Chen X, Lu Y, Wang D. 2019 Effects of heat stress on body temperature, milk production, and reproduction in dairy cows: a novel idea for monitoring and evaluation of heat stress — A review. *Asian-Australas J Anim Sci* **32**, 1332–1339. (doi:10.5713/ajas.18.0743)

43. Upadhyay RC, Singh SV, Kumar A, Gupta SK, Ashutosh. 2007 Impact of Climate change on Milk production of Murrah buffaloes. *Italian Journal of Animal Science* **6**, 1329–1332. (doi:10.4081/ijas.2007.s2.1329)

44. Gorniak T, Meyer U, Südekum K-H, Dänicke S. 2014 Impact of mild heat stress on dry matter intake, milk yield and milk composition in mid-lactation Holstein dairy cows in a temperate climate. *Archives of Animal Nutrition* **68**, 358–369. (doi:10.1080/1745039X.2014.950451)

45. Knapp DM, Grummer RR. 1991 Response of Lactating Dairy Cows to Fat Supplementation During Heat Stress. *Journal of Dairy Science* **74**, 2573–2579. (doi:10.3168/jds.S0022-0302(91)78435-X)

46. Gantner V, Mijić P, Kuterovac K, Solić D, Gantner R. 2011 Temperature-humidity index values and their significance on the daily production of dairy cattle. *Mljekarstvo : časopis za unaprjeđenje proizvodnje i prerade mlijeka* **61**, 56–63.

47. Grignolio S, Brivio F, Apollonio M, Frigato E, Tettamanti F, Filli F, Bertolucci C. 2018 Is nocturnal activity compensatory in chamois? A study of activity in a cathemeral ungulate. *Mammalian Biology* **93**, 173–181. (doi:10.1016/j.mambio.2018.06.003)

48. Büntgen U, Greuter L, Bollmann K, Jenny H, Liebhold A, Galván JD, Stenseth NC, Andrew C, Mysterud A. 2017 Elevational range shifts in four mountain ungulate species from the Swiss Alps. *Ecosphere* **8**, e01761. (doi:10.1002/ecs2.1761)

49. Loison A, Langvatn R, Solberg EJ. 1999 Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* **22**, 20–30. (doi:10.1111/j.1600-0587.1999.tb00451.x)

50. McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ. 2001 Sexual size dimorphism in fallow deer (Dama dama): do larger, heavier males gain greater mating success? *Behav Ecol Sociobiol* **49**, 266–272. (doi:10.1007/s002650000293)

51. Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2002 Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**, 165–172. (doi:10.1098/rspb.2001.1851)

52. Kruuk LEB, Slate J, Pemberton JM, Brotherstone S, Guinness F, Clutton-Brock T. 2002 Antler Size in Red Deer: Heritability and Selection but No Evolution. *Evolution* **56**, 1683–1695. (doi:10.1111/j.0014-3820.2002.tb01480.x)

53. Newbolt CH, Acker PK, Neuman TJ, Hoffman SI, Ditchkoff SS, Steury TD. 2017 Factors influencing reproductive success in male white-tailed deer. *The Journal of Wildlife Management* **81**, 206–217. (doi:10.1002/jwmg.21191)

54. Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. 2009 The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda. *Science* **325**, 464–467. (doi:10.1126/science.1173668)

55. Clutton-Brock T, Sheldon BC. 2010 Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* **25**, 562–573. (doi:10.1016/j.tree.2010.08.002)