

Decreasing litter size of marmots over time: a life history response to climate change?

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Abstract. The way that plants and animals respond to climate change varies widely among species, but the biological features underlying their actual response remains largely unknown. Here, from a 20-year monitoring study, we document a continuous decrease in litter size of the Alpine marmot (*Marmota marmota*) since 1990. To cope with harsh winters, Alpine marmots hibernate in burrows and their reproductive output should depend more on spring conditions compared to animals that are active year-round. However, we show that litter size decreased over time because of the general thinning of winter snow cover that has been repeatedly reported to occur in the Alps over the same period, despite a positive effect of an earlier snowmelt in spring. Our results contrast markedly with a recent study on North American yellow-bellied marmots, suggesting that between-species differences in life histories can lead to opposite responses to climate change, even between closely related species. Our case study therefore demonstrates the idiosyncratic nature of the response to climate change and emphasizes, even for related species with similar ecological niches, that it may be hazardous to extrapolate life history responses to climate change from one species to another.

Key words: Alpine marmot; fitness; global warming; La Grande Sassière Nature Reserve, French Alps; litter size; *Marmota marmota*; yellow-bellied marmot.

INTRODUCTION

Empirical evidence of life history responses to climate change by plants and animals has been extensively reported in recent decades (Parmesan 2006). Evidence includes changes in the phenology, demography, and the geographic distribution of species living at high altitude or latitude (e.g., Ozgul et al. 2010). However, both magnitude and direction of the response to climate change vary widely among species (e.g., Morris et al. 2008). Identifying the biological mechanisms associated with a given response to climate change is required to achieve robust projections about future biodiversity changes (Sutherland 2006). For instance, both theoretical demography (Tuljapurkar et al. 2009) and empirical comparative analyses (Morris et al. 2008) suggest that short-lived species should be more sensitive to climate change than long-lived species.

Other major characteristics of a species' life cycle are expected to reduce the effects of climate change on life histories and population dynamics. Hibernation, for instance, slows the life cycle (Turbill et al. 2011) and might buffer demographic parameters against environmental changes. Hibernating species should therefore be resistant to climate change during winter, the critical season in temperate and northern ecosystems. Accord-

ingly, a recent study carried out in the Rocky Mountains showed that the hibernating yellow-bellied marmot (*Marmota flaviventris*) benefits from earlier springs and longer growing seasons in connection with climate change (Ozgul et al. 2010). Whether similar hibernating mammals benefit from such an improvement of spring and summer environmental conditions remains unclear.

Here we used long-term monitoring of Alpine marmots, a social and hibernating mammalian rodent (see Plate 1), to test whether local weather and recent climate change influenced litter size in their highly seasonal environment. Litter size is a key life history trait in rodents (Millar 1977) that strongly influences population growth rate (Ozgul et al. 2007).

Alpine marmots live in family groups composed of a dominant pair that breeds once annually, one or several nonreproductive subordinates, and pups of the year. Marmots spend their active season accumulating enough fat both to survive hibernation during winter and to start reproduction in the following spring (Kortner and Heldmaier 1995). Litter size in mammals increases with a mother's body mass (Clutton-Brock 1991); thus, body mass at vernal emergence should be a critical determinant of marmot litter size. As hibernation should buffer marmots against harsh weather, we expected winter conditions to have little influence on litter size the following spring (Humphries et al. 2004). On the other hand, we expected earlier springs and improved spring conditions to increase litter size of Alpine marmots. Indeed, as reported in yellow-bellied marmots (Ozgul et

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al. 2010) and other taxa (Hufnagl et al. 2010), earlier springs should enable foraging females to increase body mass, which, in turn, should increase mean litter size.

METHODS

Study species and field methods

Alpine marmots hibernate from mid-October to early April. Mating occurs shortly after the end of hibernation from mid-April to early May and gestation lasts for 30 days. Once born, pups stay in the natal burrow for 40 days and emerge above ground between late June and mid-July (Appendix A; see Plate 1). The age at first reproduction is generally three years for the two sexes in our studied population. The Alpine marmot is territorial and socially monogamous, living in family groups of 2 to 15 individuals. Subordinates of the group normally do not reproduce, and subordinate males (whose number ranged from 0 to 7 per family) are called helpers because they increase pup survival during hibernation through social thermoregulation (Allainé and Theuriau 2004).

We monitored Alpine marmots of La Grande Sassièr Nature Reserve (French Alps; 45°29' N, 6°59' E; see Plate 1). From 1990 to 2011, we caught marmots each year from mid-April to mid-July using live-capture traps (Cohas et al. 2007). Individuals were tranquilized with Zolétil 100 (0.1 mL/kg; Virbac Suisse, Glattbrugg, Switzerland), marked with a numbered ear tag and a transponder (Trovan, Munich, Germany), sexed, weighed, and reproductive status assessed using scrotal or teat development. Social status is equivalent to reproductive status because only dominant individuals reproduce in this species (Hackländer et al. 2003). The number of pups produced (litter size) by dominant females was estimated from daily observations of family groups, from mid-June to mid-July (40 days after birth when they emerge from the burrow). Virtually all emerged pups were trapped within three days of emergence and mother–pups relationships were confirmed by genetic analyses (Cohas et al. 2007). We monitored a total of 241 litters from 82 different females across the study period (1990–2011). On average, 10.9 ± 4.1 (mean \pm SD) females and their litters were monitored each year.

Climatic analyses

Three seasons with a potential impact on the litter size of Alpine marmots were considered: summer at year $t - 1$ when marmots are building fat reserves from mid-June to August, winter during hibernation between December of year $t - 1$ and March of year t , and the early spring (last two weeks of April) of year t at the emergence from hibernation. We used both local weather (i.e., temperature and precipitations) and global indices (North Atlantic Oscillation index [NAO], and Normalized Differential Vegetation Index [NDVI]) to assess climate change (Martinez-Jauregui et al. 2009; see Appendix B for seasonal indices). Daily precipitation and snow

depth were recorded from the weather station of Tignes and air temperatures from Val d'Isère, both located 5 km away from the study site. Winter variables included mean temperature (i.e., monthly average of daily mean temperature), snow depth, and winter NAO from December of year $t - 1$ to March of year t . Spring variables included the mean temperature in April and the NDVI value recorded during 15 April–1 May of year t , available up to 2008 from the NOAA, with a 8×8 km resolution on a bi-weekly (on the 1st and 15th of every month) basis. We used NDVI in April, which measures plant productivity in spring (Pettorelli et al. 2005), as a proxy for the timing of snowmelt, because NDVI in spring is closely associated with snowmelt in mountain areas (Pettorelli et al. 2007). Summer variables (precipitation and primary productivity) measured at year $t - 1$ (i.e., between mid-June and August the year before litter emergence) depicted the weather experienced by Alpine marmots while building fat reserves before starting hibernation. We used the date of the maximum NDVI value (NDVI peak; Pettorelli et al. 2005) and the Bagnoul-Gaussen drought index (BGI; see e.g., Toigo et al. 2006), to assess the timing and the duration of the vegetation growth.

We used linear models to search for temporal trends in climatic variables. When a trend was detected, we used the residuals from the regression between the climate variable and year as a “de-trended variable” (a measure of the deviation of the variable from its temporal trend). Using the “de-trended” instead of the raw variable reduces the chances of spurious correlations that may arise when a trend occurs both in the response and the explanatory variable (Grosbois et al. 2008). We then fitted generalized estimating equations (GEE) models including female identity as a grouping factor to account for repeated measurements of the same individuals, and mother's age as a three-level fixed factor (unknown, prime-age, and old) to account for potential age variation in litter size. This latter model was our “baseline model” to investigate litter size in relation to time and environmental variables. We then tested for the effects of summer at year $t - 1$ and of both the winter and spring at year t on litter size. We also considered a time lag of one and two years in the response of litter size to environmental variation (Appendix C). In all models including a “de-trended” variable, year was added as a predictor variable to account for the trend (Grosbois et al. 2008).

We included additional variables to test for density dependence at the population (with density measured as the average population size divided by the number of families monitored each year) and at the family (with density measured as group size) levels, and for the effects of the number of helpers on litter size. Group size and number of helpers were available for 146 and 160 litters, respectively. We then calculated the effect of each variable in a model using an analysis of deviance (ANODEV; Skalski et al. 1993). ANODEV corresponds

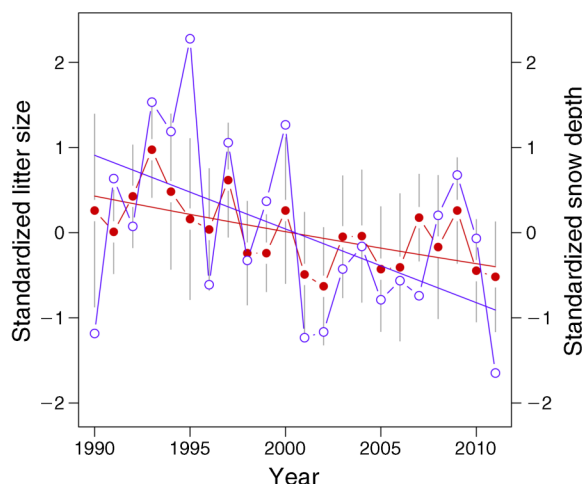


FIG. 1. Yearly variation ($\pm 95\%$ CI) in standardized litter size of Alpine marmots (*Marmota marmota*) and standardized snow cover in winter (from December to March) at La Grande Sassi re (French Alps). Litter size is represented in red (with confidence interval around the average in gray), and snow depth in blue.

to a comparison between the model including climatic covariates, vs. both the constant (i.e., baseline model) and the full time-dependent (i.e., including year as a discrete factor) models. We used generalized linear mixed models (GLMMs) to estimate the log-likelihood of each model. The corresponding F statistic tests the null hypothesis that the climatic covariate has no effect on litter size. The r^2_{dev} of the ANODEV quantifies how much of the temporal variation in average litter size is accounted for by each climatic variable.

Analyses of mechanisms behind litter size variation

Body mass variation of mothers was investigated over the period 1996–2011, when standardized measures and appropriate sample sizes to compute annual body mass were available (114 measurements of body mass over 48 females). Female body mass at emergence, the most critical parameter for reproduction, was not available because the study site is not accessible when marmots emerge in early April. We therefore corrected mother body mass by capture date, gestation status (pregnant vs. lactating), and spring conditions (average temperature and precipitation in April) using GAMMs (generalized additive mixed models) to account both for nonlinear relationship between capture date and body mass, and for repeated measurements on the same female (Tafani et al. 2013). We first tested for the effect of year (included as a covariate) on female body mass to investigate temporal changes of body mass throughout the study period. We then tested for an effect of mother body mass corrected for capture date and spring conditions on litter size ($n = 114$) with a GEE including age as a dependent variable and female identity as a

grouping factor to test for the association between female body mass and litter size.

All analyses were conducted using R version 2.14.2 (R Development Core Team 2011). Packages *geepack* (Halekoh et al. 2006), *glmmML* (Brostr m and Holmberg 2011), and *mgcv* (Woods 2006) were used to fit GEE, GLMM, and GAMM, respectively.

RESULTS

Trends of climate in our study area

Average snow depth from December to March decreased by 1.87 ± 0.68 (mean \pm SE) cm per year from 1991 to 2011 ($r^2 = 0.24$, $df = 1$, $P = 0.01$; Fig. 1) and was independent from the timing of snowmelt ($r^2 = 0.17$, $df = 1$, $P = 0.48$); while the average air temperature in April increased by $0.16 \pm 0.04^\circ\text{C}$ per year from 1990 to 2011 ($r^2 = 0.46$, $df = 1$, $P < 0.001$). Note that 1990 was an exceptionally mild winter (Durand et al. 2009), so we excluded its outlier datum to test for the temporal trend in snow depth. Data for 1990 were included in all other analyses, including analyses of litter size variation. The NAO decreased over time (-0.10 ± 0.03 , $r^2 = 0.28$, $df = 1$, $P = 0.006$) towards harsher winters with lower temperatures favoring frost but not snow. The increase in spring temperature associated with a thinning snow layer in winter we report here, matches the overall pattern of climate change in the Alps (e.g., Beniston et al. 2003; see Appendix B for seasonal indices).

Litter size variation with climatic covariates

Mean litter size of Alpine marmots varied among years ($\chi^2 = 60.2$, $df = 21$, $P < 0.01$) and decreased from 1990 to 2011 (Table 1, Fig. 1). Summer conditions before hibernation did not account for this trend and had no impact on litter size the following spring (Table 1). Mean litter size, however, was positively associated with snow depth, average air temperature and NAO the previous winter (Fig. 2, Table 1). Among those winter variables, snow cover was the main driver of observed variation in litter size over years (Table 1). As expected, litter size was positively correlated with NDVI in April (Fig. 2b, Table 1). A mild and snowy winter (from December to March) followed by an early melt of snow in April (early onset of vegetation) thus favored larger litter sizes of Alpine marmots. No first-order interactive effects between snow depth in winter, air temperature in winter, and plant productivity in April could be detected on litter size (snow \times winter temperature, $\beta = 0.027 \pm 0.041$, $P = 0.24$; snow \times April NDVI, $\beta = 0.019 \pm 0.031$, $P = 0.31$; winter temperature \times April NDVI, $\beta = 0.017 \pm 0.042$, $P = 0.43$), meaning that these variables only had additive effects on litter size of marmots. Overall, litter size was strongly influenced by environmental conditions and especially by the effect of snow depth in winter relative to plant productivity in spring. Snow depth, average winter air temperature, and NDVI in April accounted for 60% of the annual variation in litter size, with snow depth in winter accounting for 29% of the annual variation in

TABLE 1. Climatic variables accounting for observed variation in litter size of Alpine marmots (*Marmota marmota*) at La Grande Sassi re (Alps, France) between 1990 and 2011.

Parameters	1990–2008						1990–2011					
	Est.	SE	$F_{\text{cst/co/t}}$	P	r^2_{dev}	r^2_{tot}	Est.	SE	$F_{\text{cst/co/t}}$	P	r^2_{dev}	r^2_{tot}
Year	−0.012	0.006	6.54	0.020	0.28	0.28	−0.011	0.005	7.71	0.012	0.28	0.28
Winter												
(Year) + <i>winter NAO</i>	0.054	0.028	5.87	0.025	0.23	0.23
(Year) + <i>winter snow cover</i>	0.057	0.022	11.70	0.003	0.37	0.37
(Year) + <i>winter temperature</i>	0.020	0.019	0.77	0.390	0.04	0.06
Spring												
April NDVI	0.070	0.031	6.75	0.019	0.28	0.28
(Year) + <i>April temperature</i>	0.036	0.023	2.14	0.159	0.10	0.10
Summer												
Summer NDVI peak ($t - 1$)	0.023	0.021	1.40	0.253	0.07	0.07
Summer Gaussen index ($t - 1$)	0.015	0.020	1.20	0.284	0.06	0.06
All												
(Year) + <i>winter snow cover</i>	0.054	0.024	10.01	0.006	0.29	0.51
+April NDVI	0.056	0.033	7.67	0.013	0.22
(Year) + <i>winter snow cover</i>	0.068	0.023	14.98	0.009	0.37	0.51
+ <i>Winter temperature</i>	0.038	0.020	9.78	0.028	0.14	...
(Year) + <i>winter snow cover</i>	0.057	0.025	12.37	0.003	0.29	0.60
+April NDVI	0.047	0.035	9.48	0.007	0.22
+ <i>Winter temperature</i>	0.026	0.021	4.02	0.061	0.09

Notes: “De-trended” variables, entered in the model with their trend stated as “(Year)”, appear in italics. Global indices are the North Atlantic Oscillation index (NAO) and Normalized Differential Vegetation Index (NDVI). Climatic effects were tested with an analysis of deviance (ANODEV, see *Methods* for details). The F statistic of ANODEV (noted $F_{\text{cst/co/t}}$) and its associated value (P) test the climatic covariate effect on litter size, while r^2_{dev} provides a measure of its magnitude. The total r^2 of a model with several covariates is denoted as r^2_{tot} . Statistically significant variables are in boldface ($P < 0.05$). Because NDVI values are released with a delay (last measure available in 2008), we replicated our analyses from 1990 to 2008 when data were not available and from 1990 to 2011 (i.e., when NDVI was not included in the model).

litter size vs. 22% for plant productivity in spring (Table 1). No lagged effects of any climatic variable were detected on litter size (see Appendix C). Similarly, there were no detectable effects of population size, group size, or the number of helpers on litter size the following spring (population size, $\beta = 0.022 \pm 0.022$, $P = 0.31$; group size, $\beta = -0.025 \pm 0.034$, $P = 0.45$; number of helpers, $\beta = -0.012 \pm 0.035$, $P = 0.74$).

Mother body mass and litter size variation

As expected, litter size increased with residual mother body mass, a proxy of female condition ($\beta = 0.112 \pm 0.037$, $P = 0.002$), indicating that heavier females were more likely to produce larger litters than were lighter ones. Once the positive effects of spring conditions on body mass were accounted for (April temperature, $\beta =$

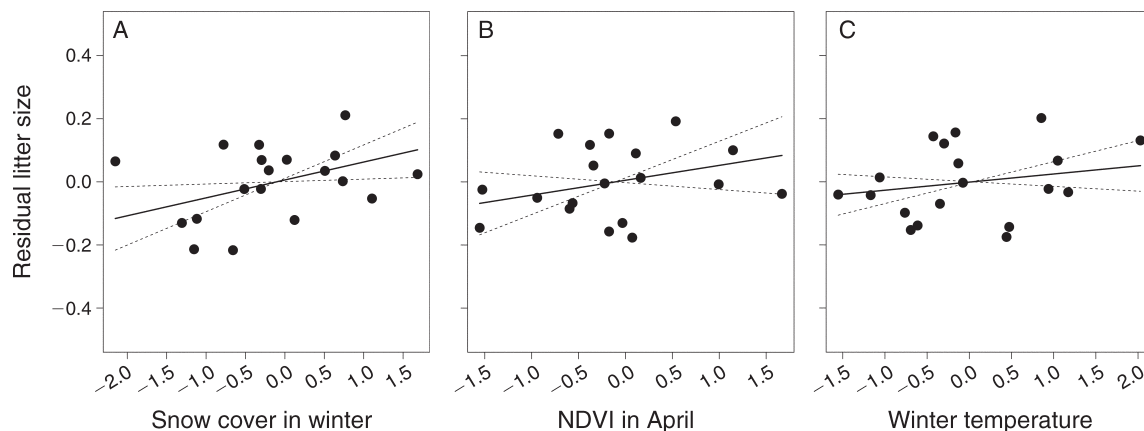


FIG. 2. Effects of the average snow cover and winter temperature from December to March and of the Normalized Differential Vegetation Index (NDVI) in April on litter size of Alpine marmots at La Grande Sassi re (French Alps) between 1990 and 2011. Dots represent (A) residual litter size per standardized snow depth value after controlling for the linear annual trend (year as a linear variable), (B) residual litter size per standardized NDVI in April after accounting for the effect of snow depth, and (C) residual litter size per standardized winter temperature value after accounting for the snow depth and NDVI in April effects. Lines represent the model predictions (solid, bold) and their associated confidence intervals (dashed).



PLATE 1. (Upper) Alpine marmot pup a few days after its first emergence from the burrow, in early July. (Lower) La Grande Sassi re Nature Reserve (French Alps) in early July. Photo credits: marmot, Marie-L a Travert; landscape, Lumi re des Alpes.

200.58 ± 42.24 , $P = 0.006$; April precipitation, $\beta = 96.57 \pm 42.53$, $P = 0.06$), mother body mass tended to decline over time ($\beta = -19.96 \pm 9.72$, $P = 0.07$; Fig. 3). Thus, female marmots were likely to emerge from hibernation with a lower body condition in recent years than in the 1990s.

DISCUSSION

Patterns of litter size variation with climate change

Unexpectedly for a hibernating species, snow depth in winter was the main driver shaping litter size of Alpine marmots (Table 1). This is supported by two lines of evidence. First, the long-term decline in snow depth during winter (Fig. 1; see Beniston et al. 2003 for a similar observation in the Alps) is concomitant with the

decline of litter size. Second, the average snow depth during winter accounts for slightly higher temporal variation in litter size than any other weather variables we analyzed (Table 1). The apparent decline of mother body mass over the same period suggests that female body mass was involved in the decline in litter size we report (Fig. 3). During hibernation, Alpine marmots have to spend energy for maintaining body temperature above 5 C (Arnold et al. 1991). A thinner snow cover during winter reduces the insulation layer, leading frost to reach deep underground (Appendix D) and increasing marmot's fat depletion. Conversely to winter conditions, litter size was positively correlated with spring NDVI, a measure of snowmelt timing in our study. Earlier snowmelt shortens the period of time between hibernation and access to high-quality food (Ozgul et al. 2010)

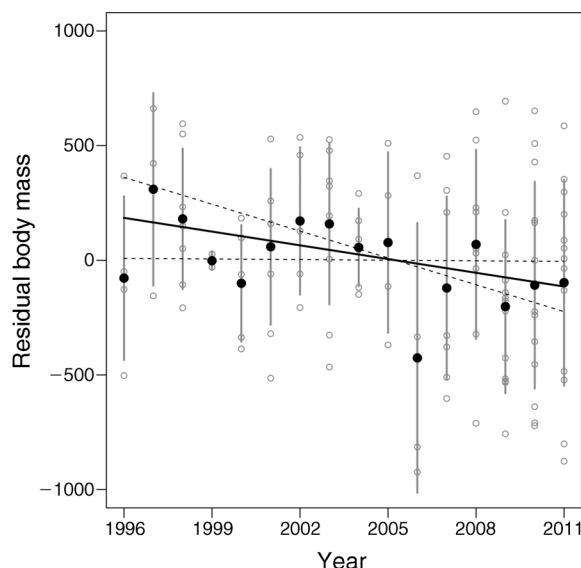


FIG. 3. Annual variation ($\pm 95\%$ CI) in residual body mass of female Alpine marmots at La Grande Sassi re (French Alps) between 1996 and 2011, after accounting for possible confounding effects of capture date, gestation status (pregnant vs. lactating), and spring conditions (April temperature and precipitations). Solid circles represent the average residual body mass per year across all females with their standard error bars (gray). Lines represent the regression of residual body mass through time (solid, bold) and its associated confidence interval (dashed).

so that marmots are in better condition at emergence. Climate change affects litter size of Alpine marmots in a complex way and, in the long run, an earlier onset of spring conditions could buffer variation in reproduction caused by winter harshness.

Idiosyncratic responses to climate: details matter

The trend we found in litter size of Alpine marmots contrasts with the increase of population size reported recently for the closely related yellow-bellied marmot (Ozgul et al. 2010). The long-term average of snow layer at Gothic, Colorado, USA (Rocky Mountains) was considerably thicker and lasted much longer than at La Grande Sassi re (respectively 426 vs. 99 cm and from October to late May vs. November to late April). Yellow-bellied marmots could then benefit from a better and longer thermal insulation while hibernating than Alpine marmots (see Appendix D). Moreover, yellow-bellied marmots have a lower metabolism at a given temperature (Armitage et al. 2003) and might thus be more efficient in saving energy during hibernation. The combination of a thinner snow layer and less efficient hibernation likely leads Alpine marmots to deplete fat reserves faster than yellow-bellied marmots, and hence to emerge in a lower body condition when winter conditions are harsh. Accordingly, we observed a decline in body mass of female Alpine marmots over years (Fig. 3). Given the positive effect of female body mass on

litter size, the decrease in female mass through time (Fig. 3) likely accounts for the observed decline in litter size.

The association between winter climate (snow cover) and litter size we report for Alpine marmots might also be related to social hibernation (Arnold 1993). In social living species, group size and composition during hibernation can influence energy expenditures of group members. Under harsh conditions, hibernating with two to three helpers (i.e., subordinate males) can substantially improve the overwinter survival of pups (Allain  and Theuriau 2004). Smaller litters could decrease the number of helpers in subsequent years. A potential drawback of the reduced number of helpers could be a decrease of the overwinter survival of pups. Alpine marmots could thus enter a vicious cycle caused by multiplicative effects of climate on their reproductive output.

Striking differences between closely related species of marmots stress the potential pitfalls of extrapolating life history responses to climate change at different locations or across species. We thus encourage additional long-term individual-based studies designed to gain insights into the relationship between climate and life history variation (Mart nez-Jauregui et al. 2009). Differences among species in life history strategy can be critical in their demographic and population dynamic responses to global change.

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SUPPLEMENTAL MATERIAL

Appendix A

Alpine marmot (*Marmota marmota*) life cycle ([Ecological Archives E094-050-A1](#)).

Appendix B

Complementary analyses using seasonal indices ([Ecological Archives E094-050-A2](#)).

Appendix C

Complementary analyses of lagged effects ([Ecological Archives E094-050-A3](#)).

Appendix D

Additional information on burrow temperature and efficiency of snow insulation during winter ([Ecological Archives E094-050-A4](#)).