



Differential plasticity of size and mass to environmental change in a hibernating mammal

Canale, Cindy I; Ozgul, Arpat; Allainé, Dominique; Cohas, Aurelie

Abstract: Morphological changes following changes in species' distribution and phenology have been suggested to be the third universal response to global environmental change. Although structural size and body mass result from different genetic, physiological, and ecological mechanisms, they are used interchangeably in studies evaluating population responses to environmental change. Using a 22-year (1991-2013) dataset including 1768 individuals, we investigated the coupled dynamics of size and mass in a hibernating mammal, the Alpine marmot (*Marmota marmota*), in response to local environmental conditions. We (i) quantified temporal trends in both traits, (ii) determined the environmental drivers of trait dynamics, and (iii) identified the life-history processes underlying the observed changes. Both phenotypic traits were followed through life: we focused on the initial trait value (juvenile size and mass) and later-life development (annual change in size [Δ size] and mass [Δ mass]). First, we demonstrated contrasting dynamics between size and mass over the study period. Juvenile size and subsequent Δ size showed significant declines, whereas juvenile mass and subsequent Δ mass remained constant. As a consequence of smaller size associated with a similar mass, individuals were in better condition in recent years. Second, size and mass showed different sensitivities to environmental variables. Both traits benefited from early access to resources in spring, whereas Δ mass, particularly in early life, also responded to summer and winter conditions. Third, the interannual variation in both traits was caused by changes in early life development. Our study supports the importance of considering the differences between size and mass responses to the environment when evaluating the mechanisms underlying population dynamics. The current practice of focusing on only one trait in population modeling can lead to misleading conclusions when evaluating species' resilience to contemporary climate change.

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1 **Differential plasticity of size and mass to environmental change in a hibernating**
2 **mammal**

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4 Running head: Differential plasticity of size and mass

5

6 CINDY I. CANALE¹, ARPAT OZGUL¹, DOMINIQUE ALLAINÉ², AURELIE COHAS²

7

8 *¹ Department of Evolutionary Biology and Environmental Studies, University of Zurich,*
9 *Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*

10 *² UMR-CNRS 5558, Laboratoire de Biométrie et Biologie Evolutive, Université Claude*
11 *Bernard, Lyon 1, 43 Bd. du 11 novembre 1918, F-69622 Villeurbanne Cedex, France*

12 Correspondence: Cindy I. Canale, tel. +41 44 63 54911, fax: +41 44 63 54780, e-mail:

13 cindy.canale@ieu.uzh.ch

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17

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19 **Abstract**

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22 structural size and body mass result from different genetic, physiological and ecological
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26 marmot (*Marmota marmota*), in response to local environmental conditions. We (i) quantified
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32 size and subsequent Δ size showed significant declines, whereas juvenile mass and subsequent
33 Δ mass remained constant. As a consequence of smaller size associated with a similar mass,
34 individuals were in better condition in recent years. Second, size and mass showed different
35 sensitivities to environmental variables. Both traits benefited from early access to resources in
36 spring, whereas Δ mass, particularly in early life, also responded to summer and winter
37 conditions. Our study supports the importance of considering the differences between size and
38 mass responses to the environment when evaluating the mechanisms underlying population
39 dynamics. The current practice of focusing on only one trait in population modelling can lead
40 to misleading conclusions when evaluating species' resilience to contemporary climate
41 change.

42 **Introduction**

43 Climate change is affecting population dynamics of numerous species, but the intrinsic
44 mechanisms by which these responses arise remain under-studied (Parmesan, 2006; Somero,
45 2012). An understanding of the mechanistic relationships between environmental variables
46 and species' demographic responses is needed to reliably predict organisms' vulnerability to
47 climate change (Seebacher *et al.*, 2012). Fitness-related phenotypic traits, acting as state
48 variables, could provide such a mechanistic link (Huey *et al.*, 2012, Ozgul *et al.* 2014). These
49 traits are strongly related to an individual's reproductive success and survival; thus,
50 phenotypic distributions are expected to change and influence population dynamics in
51 response to environmental change (Kearney *et al.*, 2009; McMahon *et al.*, 2011). Phenotypic
52 traits such as structural size and body mass play a pivotal role. First, changes in animal body
53 size have recently been claimed to be the third universal response to contemporary climate
54 change in addition to changes in distribution and phenology (Gardner *et al.*, 2011; Sheridan *et*
55 *al.*, 2011). Second, their responses to climate change can occur on a short time scale (Gienapp
56 *et al.*, 2008; Boutin *et al.*, 2014). Third, structural size and body mass affect population
57 performances of vertebrates through their direct impact on individual life-histories (Schmidt-
58 Nielsen, 1984; Blackburn *et al.*, 1994; Smith *et al.*, 2013).

59 Despite evidence of climate-driven changes in endotherms' body traits that has
60 accumulated over the last decades, their environmental drivers remain hotly debated (McNab,
61 2010; Gardner *et al.*, 2011; Yom-Tov *et al.*, 2011). However, modifications in nutritional
62 and/or thermal environment can be seen as the two major drivers (Millien *et al.*, 2006;
63 McNab, 2010). On one hand, climate related changes in the availability or quality of food can
64 have a direct impact on trait changes through modulation of the energy input (McNab, 2010).
65 For instance, positive trends in size have been associated with earlier vegetation onset and
66 longer growing season (Yom-Tov *et al.*, 2004; Yom-Tov *et al.*, 2005; Ozgul *et al.*, 2010;

67 Yom-Tov *et al.*, 2010c; Eastman *et al.*, 2012), whereas negative ones have been associated
68 with lower primary productivity (Hersteinsson *et al.*, 2009; Sheridan *et al.*, 2011). On the
69 other hand, a rise in ambient temperature over a critical thermal limit can have a direct
70 consequence on body traits through increasing energy expenditure. Negative size trends have
71 been suggested to be a response to these new thermoregulatory constraints, assuming that heat
72 dissipation is more efficient in smaller bodied species as surface area to volume ratio is
73 reduced (Post *et al.*, 1997; Smith *et al.*, 1998; Yom-Tov *et al.*, 2010a), in line with
74 Bergmann's rule (Bergman, 1847). Despite the various environmental drivers involved,
75 previous studies clearly demonstrate that a disruption of the energy balance can be a common
76 feature of trait shifts, and the variation in responses observed in terms of direction and
77 magnitude could result from differences in exposure and sensitivities (Ashton *et al.*, 2000;
78 Millien *et al.*, 2006; Meiri, 2011; Teplitsky *et al.*, 2014).

79 Structural size and body mass are often used interchangeably to evaluate organisms'
80 responses to environmental change, especially in trait-based demographic models, although
81 they result from energy allocation to different functions (Piersma *et al.*, 1991). In most
82 endotherms, skeletal size is a reserve-independent structural measure resulting from the
83 allocation of resources to growth during development (Calder, 1984; Hou *et al.*, 2008). From
84 birth, individual size increases follow a logistic curve function of the environmental
85 conditions until a maximum is reached at adulthood (Monaghan, 2008). However, some
86 exceptions concerning peculiar skeletal structures exist, such as a seasonal shrinkage of the
87 braincase observed in soricine shrews and arvicoline rodents living in cold temperate areas
88 (Dehnel phenomenon; Dehnel, 1949; Pucek 1963; McNab, 1999). On the other side, body
89 mass, which is a composite of structural mass including bones, organs, skin, blood, skeletal
90 muscle, and storage mass (Wang *et al.*, 1992; Hume *et al.*, 2002; Fosbøl *et al.*, 2015), is a
91 crude but widely used estimate of nutrient energy reserve. It is a dynamic trait that can change

92 repeatedly throughout life to maximize survival and/or subsequent reproductive output
93 (Heldmaier, 1989). These distinctions between structural size and body mass may lead to
94 different interpretations of population responses to environmental conditions at different life
95 stages. Unfortunately, most studies are still focusing only on one trait and on particular life
96 stages (Allainé *et al.*, 1998; Pettorelli *et al.*, 2002, but see Cooch *et al.*, 1991; Guillemain *et*
97 *al.*, 2005; Rode *et al.*, 2010; Nielsen *et al.*, 2013).

98 Despite the recent interest in investigating climate-related morphological changes in
99 wild populations, underlying ecological and evolutionary mechanisms remain rarely
100 investigated (Boutin *et al.*, 2014; Teplitsky *et al.*, 2014). Observed body size shifts can be
101 mediated through phenotypic plasticity and/or through selection if the trait is heritable
102 (Coulson & Tuljapurkar, 2008; Boutin *et al.*, 2014; Kopp *et al.*, 2014). The former is the
103 ability of the same genotype to express different phenotypes under different environmental
104 conditions within a lifespan, whereas the latter involves directional genetic changes with
105 survival or reproductive selection acting on the phenotype over generations (Merilä *et al.*,
106 2014). Plasticity can also evolve if present reaction norms have a genetic basis (Dejong,
107 1995). Recent studies focusing on body mass have shown that phenotypic plasticity plays an
108 important role in observed changes in body mass distributions (Teplitsky *et al.*, 2008; Ozgul
109 *et al.*, 2009; Husby *et al.*, 2011). Conflicting selection pressures are expected on skeletal
110 growth and body mass fluctuations, as a specific set of genes is associated with adult stature
111 and mass, and another independent set of genes is regulating the rate of growth in body size
112 (Janz, 2004; Marroig *et al.*, 2010). Given the small number of mammal species studied and
113 the limited time frame of these studies, our understanding of whether species will be able to
114 tolerate the speed and magnitude of ongoing environmental change is limited (Williams *et al.*,
115 2008; Hoffmann *et al.*, 2011).

116 Alpine species, subject to extreme environmental change over the last decades, are
117 expected to represent excellent indicator species that could help anticipate organisms'
118 vulnerability to climate change and thus forecast likely future impacts on biodiversity
119 (Theurillat *et al.*, 2001; Yoccoz *et al.*, 2010; Büntgen *et al.*, 2014). During the last century, the
120 Alps have shown a 2°C increase in minimal temperature while summer precipitation and
121 winter snowfall have decreased drastically (Keller *et al.*, 2005; Beniston, 2006). Due to their
122 adaptation to extreme and very specific conditions, endemic alpine species are particularly
123 vulnerable to climate change (Davis, 2005; Maiorano *et al.*, 2013), and dramatic
124 consequences have already been detected in vegetation community compositions (Engler *et*
125 *al.*, 2011). In this context, the Alpine marmot (*Marmota marmota*), an endemic hibernating
126 mammal of the Alps, provides a unique opportunity to study the joint dynamics of structural
127 size and body mass in response to climate change. Using a 22-year dataset (1991-2013) of
128 individual structural size and body mass measurements, we quantified temporal trends in both
129 traits, determined environmental drivers of trait dynamics, and identified the life-history
130 processes underlying the observed changes.

131

132 **Materials and methods**

133 *Model species*

134 The Alpine marmot is a hibernating ground-dwelling squirrel; it lives in family groups from 2
135 to 20 individuals, composed of a dominant pair (≥ 3 years old), sexually mature adults (≥ 3
136 years old), subadults (age 2 to 3) and yearlings (age 1 to 2) subordinates, and juveniles (age 0
137 to 1) (Allainé, 2000). A family group occupies a territory (2.5 ± 0.53 ha, Perrin *et al.*, 1993)
138 including a main burrow and side burrows. It is socially monogamous, and within family
139 groups reproduction is monopolized by the dominant pair (Arnold, 1990a,b; Cohan *et al.*,

140 2008; Lardy *et al.*, 2012). Dominants inhibit reproduction of same-sex subordinates through
141 aggressive behaviour (Arnold *et al.*, 1997; Hackländer *et al.*, 2003).

142 Within a family group, marmots hibernate together from mid-October to early April
143 (Arnold, 1990b). Hibernation plays a central role in their life history. Accumulation of fat
144 during the active period and loss of it during hibernation (Körtner & Heldmaier, 1995)
145 determines winter survival and subsequent reproductive success (Tafari *et al.*, 2013).
146 Subordinate males are called helpers as they increase pup survival during hibernation through
147 thermal benefits of synchronized arousals and active warming (Arnold, 1993; Ruf & Arnold,
148 2000; Allainé & Theuriau, 2004). Minimal energy expenditure during hibernation has been
149 defined over a burrow temperature range from 5°C to 15°C (Arnold *et al.*, 1991; Ortmann &
150 Heldmaier, 2000). Below the critical threshold of 5°C, energy expenditure increases linearly;
151 for instance, at a burrow temperature of 0°C, minimal metabolic rate during torpor is already
152 four times higher than the torpid metabolic rate (Arnold *et al.*, 1991). Mating occurs in mid-
153 April shortly after the hibernation period (Müller-Using, 1957; Psenner, 1957; Hemberck,
154 1958). Then, dominant females are pregnant for 30 days and give birth to a litter of 1 to 7
155 juveniles (median = 4) and nurse them for another 40 days underground in the natal burrow.
156 Juveniles first emerge above ground at weaning (Psenner, 1957), which in our study
157 population occurs between late June and mid-July (Allainé *et al.*, 1998).

158

159 *Field procedures*

160 We monitored a wild population of Alpine marmots located in a typical alpine meadow of the
161 Grande Sassièrè nature reserve (2340 m a.s.l., French Alps, 45°29'N, 6°59'E), from 1990 to
162 2013. Marmots belonging to 26 family groups (*i.e* territories) have been captured every year
163 from mid-April to mid-July using two-door live traps (100 x 25 x 25 cm, Tomahawk Live
164 Trap, Hazelhurst, WI, U.S.A), baited with dandelions (*Taraxacum officinale*) and placed near

165 the entrances of the main burrows in order to assign each captured individual to its family
166 group. Once captured, individuals were anaesthetised with Zolétil 100 (0.1 ml.kg⁻¹). At first
167 capture (as pup or immigrant), all marmots were individually marked using a transponder and
168 a numbered metal ear-tag placed on the right ear of females and on the left ear of males. An
169 additional coloured plastic ear tag was placed on the opposite ear of dominant individuals.
170 Animal identity, sex, age, reproductive status, social status and body measurements (see
171 below) were recorded at each capture. Age class was determined according to known birth
172 date or to body shape (up to three years). Immigrants were assigned to the adult age class as
173 they are known to disperse after two years old (Arnold, 1990a). Social status was determined
174 according to scrotal development for males and teat development for females and then
175 confirmed by behavioral observations as dominant pairs predominantly initiate aggressive
176 interactions (Arnold & Dittami, 1997) and scent-mark their territories by regular cheek
177 rubbing behavior (Bel et al. 1999). In addition, both hair samples and skin biopsies were
178 collected on all trapped individuals for genetic analysis.

179 Helper presence or absence and identity of the dominant pair were obtained by
180 intensive observations of each family group (see Cohas *et al.* 2008 for details on observations
181 protocol). As weaning occurs when pups first emerge from their natal burrow, the date of
182 weaning and litter size at weaning (hereafter, litter size) in each family was determined from
183 daily observations. Virtually all emerged offspring were either trapped with smaller two-door
184 live traps or caught by hand within three days of emergence. Data collection was consistent
185 across the 24 years as the project was consistently supervised by two of us (DA, AC).

186

187 *Annual structural size and body mass determination*

188 Structural size was the measure of body length (hereafter, size) from snout to the base of the
189 tail (± 0.5 cm with a measuring tape). Body mass (hereafter, mass) was obtained by weighing

190 all captured individuals (± 5 g for juveniles, ± 25 g for older individuals) with a Pesola spring
191 balance. Marmot measurements showed strong intra-annual change that varied substantially
192 between sex, age class, reproductive and social status (Körtner & Heldmaier, 1995; and see
193 figures in Appendix S1 for the present study). To account for the pronounced intra-annual size
194 and mass variations within each age, sex, social and reproductive status, we estimated both
195 traits for each individual for a fixed day-of-year. We predicted juvenile size and mass
196 according to the age they had on July 14 (195th day-of-year), which is the latest weaning date
197 observed during the study period. For older age classes, we used the fitted models to predict
198 size and mass on July 1 (182nd day-of-year). July represents the end of the reproductive period
199 and the majority of the data were collected around this date, providing a better estimate for
200 both size and mass (see Appendix S1 for further details on the estimation). For the rest of the
201 analyses, we used estimated values of log-transformed size and mass for each individual and
202 year.

203

204 *Environmental variables*

205 In mammals, structural size and mass are key phenotypic traits influencing survival and
206 reproductive success. Thus, we focused on environmental variables known to affect survival
207 (Farand *et al.*, 2002; Rézouki *et al.*, unpublished data) and reproductive output (Tafari *et al.*,
208 2013) in this species.

209 Three seasons with differential impacts on Alpine marmots' size were considered: (1)
210 summer (July-August), when marmots build fat reserves, (2) winter (December-March), when
211 marmots hibernate, and (3) early spring (last two weeks of April), when marmots emerge
212 from hibernation in our study area. For climatic factors, we used both local weather and
213 Normalized Differential Vegetation Index (NDVI, Pettorelli *et al.*, 2005). Daily ambient
214 temperature, precipitation, and snow depth were recorded from Météo France weather stations

215 situated within 5km from the field site, respectively Val d'Isère (1840m), Tignes Brevières
216 (1560 m) and Tignes (2080m). NDVI provided by the National Oceanic and Atmospheric
217 Administration was obtained from the AVHRR data set (1990-2000) within an 8x8 km pixel
218 area and the MODIS data set (2001-2013) with a resolution of 1x1 km pixel centered on the
219 study site. Summer variables included a summer condition index measured as the July to
220 August Bagnouls-Gausson aridity index (BGI, total daily rainfall (mm) minus twice the mean
221 ambient temperature (°C) (Dajoz, 1973; high aridity is represented by low BGI value). This
222 summer condition index is a measure of the conditions for vegetation growth and thus a good
223 proxy of the quality of green forage (Basso *et al.*, 2012). It has been repeatedly related to
224 herbivore performance (Gaillard *et al.*, 1997; Garel *et al.*, 2004; Toïgo *et al.*, 2006). Winter
225 variables included mean snow depth (*i.e.* average of daily accumulated snow depth between
226 December and March) as a proxy for burrow insulation and mean winter temperature (*i.e.*
227 average of daily mean temperature). Spring variables included the NDVI value recorded
228 during April 15 to May 1, which measures plant productivity (Pettorelli *et al.*, 2007). NDVI
229 was used as a proxy of the onset of vegetation (Hamel *et al.*, 2009) and thus of food
230 availability at the time of hibernation emergence, when food availability is crucial. High April
231 NDVI values represent early vegetation onset, whereas low April NDVI values represent late
232 vegetation onset. Note that the effects of spring and summer air temperature were not
233 considered, as buffered burrows represent a way-out to thermoregulatory constraints.

234 We used linear models to search for temporal trends in climatic variables. Indeed,
235 correlation between the trait and environmental variables may arise because both are changing
236 through time but without a causal link between them. When a trend was detected, we used the
237 residuals from the regression between the climate variable over year as a “de-trended
238 variable” (a measure of the deviation of the variable from its temporal trend). Using the “de-
239 trended” instead of the raw variable reduces the chances of spurious correlations (Grosbois *et*

240 *al.*, 2008). Only the winter temperature variable showed a significant linear temporal trend
241 during the study period ($-0.089 \pm 0.032 \text{ } ^\circ\text{C}\cdot\text{year}^{-1}$, $p=0.012$).

242

243 *Size and mass dynamics*

244 We omitted the first two years owing to lower sampling effort. From 1992 to 2013, we
245 recorded 1829 measures of size and 2276 measures of mass on 1768 individuals.

246

247 *Base models.* We performed age-specific analyses using linear mixed models. For juveniles,
248 we modeled size and mass, which provided the initial trait values. For later age-classes, we
249 modeled the annual changes in size ($\Delta\text{size} = \text{size}_{t+1} - \text{size}_t$) and mass ($\Delta\text{mass} = \text{mass}_{t+1} - \text{mass}_t$)
250 defined as the difference in trait value from one year to the next. We modeled Δsize and
251 Δmass conditional on initial size and mass, respectively (*i.e.* $\Delta\text{size} \sim \text{size}_t$ and $\Delta\text{mass} \sim \text{mass}_t$;
252 see Fig. S1 and Table S1 for details). It is important to note that change in body mass is a
253 composite measure and includes changes in bones, organs, skin, blood, skeletal muscle, and
254 storage mass (Wang *et al.*, 1992; Hume *et al.*, 2002; Fosbøl *et al.*, 2015). Note that we chose
255 not to use a body condition index as their use remains hotly debated (Green, 2001; Peig &
256 Green, 2010). Body mass alone provides a better indicator of nutrient reserves than an
257 unverified size-adjusted index (Schamber *et al.*, 2009). Because adult skeletal size is reached
258 at three years old (see Fig. A1 in Appendix S1), subadult Δsize was measured as the
259 difference in size between age two and their first capture as adults (\geq age 3). Subadult Δmass
260 remained as the difference in mass between ages two and three. Fitted values obtained from
261 these models will be referred to as Δsize and Δmass respectively.

262 Our analyses needed to account for the possibility that several variables would
263 confound trait responses to the environment. Thus, we included as fixed effects variables
264 known to affect Alpine marmots' size and mass, namely sex (in all age class models), litter

265 size and date of weaning (in the juveniles models only), and social status (subordinate or
266 dominant in the adults models only). For juveniles, we also accounted for the helper presence
267 since they have a direct impact on juveniles' energy expenditure during hibernation (Arnold,
268 1993). For older individuals, we accounted for an interactive effect between the presence of
269 juveniles and sex. Indeed, during the hibernation period, males arouse more often and earlier
270 than females, thus paying a heavier energetic cost (Arnold, 1990b). Territory aspect was also
271 considered since, in Alpine habitats, south-facing slopes receive more direct sunlight than
272 north-facing ones, leading to faster snow melt with direct consequences on vegetation growth.

273 We further included marmot territories as a random effect on the intercept of each age-
274 specific model and marmot identity in adult models, to account for spatial and individual
275 heterogeneity generated by repeated measurements on the same territories and on the same
276 animals (*i.e.* repeated sampling on the same adult individual in consecutive years).

277

278 *Inter-annual variation and long-term temporal trends.* First, we assessed inter-annual
279 variation using a global χ^2 test comparing a general model accounting for temporal variation
280 in both traits by including year as a discrete factor, and a constant model with no fixed effect
281 of year, both accounting for the confounding variables described above (Table S1). We
282 calculated the percentage of inter-annual variation explained by the factor 'year' as the ratio
283 of the difference in deviance between the general and the constant model to the deviance of
284 the constant model multiplied by 100. Our second analysis was designed to describe the long
285 term temporal trend by including year as a continuous variable and accounting for the
286 confounding variables described above in a linear regression analyses (Table S1). We used an
287 analysis of deviance (ANODEV; Skalski, 1996) to quantify the percentage of inter-annual
288 variation in mean trait value that was explained by long-term temporal trends. We calculated
289 this proportion as $R^2_{\text{dev}} = [\text{Dev}_{\text{constant}} - \text{DEV}_{\text{cova}}] / [(\text{Dev}_{\text{constant}} - \text{Dev}_{\text{FACyear}})]$, where 'constant'

290 indicates the reduced model built under the hypothesis of no temporal variation, ‘cova’
291 indicates the covariate model where the temporal variation is accounted for by year as a
292 continuous variable and ‘FACyear’ the model with year as a factor (*i.e.* full time-dependent).
293 The percentage of variance explained was obtained by multiplying R^2_{dev} by 100.

294

295 *Environmental effects.* In juveniles, we tested for the effects of vegetation onset (April NDVI)
296 during their birth year (year t) on their size and mass. In older age classes, we tested summer
297 condition index (BGI) at year t and both the effects of winter severity (snow depth and
298 temperature) and vegetation onset (April NDVI) at year $t+1$ on their Δ size and Δ mass. All of
299 the environmental variables were mean-centered and standardized to allow for a comparison
300 of their relative effects. In all models including the “de-trended” winter temperature, year was
301 added to account for the trend (Grosbois *et al.*, 2008). Only additive effects were considered,
302 except from interactive effects of vegetation onset and the date of weaning, and of vegetation
303 onset and litter size of juveniles. Indeed, there are two main constraints on juvenile size and
304 mass. When pups endure higher energetic constraints either due to late weaning or larger litter
305 size we expected food availability to have a stronger impact. In the adult model, we tested for
306 the interaction of social status and all environmental variables to estimate differential impact
307 between dominant and subordinate adults (Table S2).

308 We checked for multicollinearity and found no correlation among environmental
309 variables (Table S3, S4). For each age class, we generated a set of models with all possible
310 combinations of model terms of interest (*i.e.* summer condition index, winter temperature,
311 winter snow depth, vegetation onset) taking into account the stage-specific confounding
312 variables (defined above in the base model) (Table S5). We selected models based on the
313 Akaike information criterion corrected for small sample size (AICc)(Burnham *et al.*, 2002).

314 When alternative models were indistinguishable ($\Delta AIC_c < 2$), the model with fewer parameters
315 was retained (Burnham *et al.*, 2002).

316 Next, an ANODEV was used to quantify how much of the temporal variation in mean
317 trait value was accounted for by each environmental variable. The percentage of variance
318 explained was calculated similarly as above: $R^2_{dev} = [Dev_{constant} - DEV_{cova}] / [(Dev_{constant} -$
319 $Dev_{FAC_{year}})] * 100$. To evaluate the proportion of the variance explained by a specific
320 environmental variable, the covariate model (subscripted 'cova') included the focal climatic
321 covariate as a continuous variable.

322

323 *Life-history processes underlying trait changes*

324 To understand the processes underlying the observed phenotypic change, we decomposed the
325 change in mean trait value into contributions from selection and other processes using the
326 age-structured Price equation (ASPE, Coulson & Tuljapurkar, 2008). We applied the ASPE to
327 a sample that includes 1090 females with known weaning date and mother identity. Mother
328 identity was determined by field observations confirmed by genetic parentage analysis
329 conducted on 16 microsatellite loci (methods and microsatellite characteristics details are
330 provided in Cohas *et al.*, 2008). The exact change in mean value of a trait over a time step is
331 decomposed into seven contributions. The mathematical details are provided in Coulson &
332 Tuljapurkar (2008) and Ozgul *et al.* (2009). Here, we provide further details on the
333 interpretation of terms. The *DCs* term describes change resulting from changes in
334 demographic composition due to ageing, whereas the *DCr* term describes the change resulting
335 from the addition of new individuals due to birth. The *VS* term is the viability selection
336 differential on the trait; it describes how selective removal of individuals through mortality
337 alters the mean trait value. The contribution of age-specific trait development (i.e., growth or
338 reversion) among individuals that survive is captured in the *GR* term. The *FS* term is the

339 reproductive selection differential; it describes how selective reproduction of individuals
340 alters the mean trait value. The *OMD* term represents the contribution of differences between
341 offspring and parental trait values to observed change plus the contribution from any
342 covariance between *OMD* and number of offspring produced by each individual. Each of
343 these terms is weighted by demographic sensitivities, which describes how survival or
344 reproduction in an age class contributes to population growth. We applied the ASPE to annual
345 fluctuations observed in size and mass separately.

346

347 All analyses were conducted in R 3.1.0 (R Core Team, 2014). Linear mixed models
348 were fitted using the package ‘lme4’ (Bates *et al.*, 2012). We used the function dredge in the
349 package ‘MuMin’ to generate a set of models with all possible terms combinations (Barton *et al.*,
350 2015) and the package ‘Effects’ to obtain fitted values, partial residuals and standard error
351 estimates of mixed models on the predictor of interest (Fox, 2003; Fox *et al.*, 2009).

352

353 **Results**

354 *Inter-annual variations and long-term temporal trends*

355 Size, mass, Δ size and Δ mass strongly varied between years ($df=21$, all $\chi^2 < 0.001$).
356 Inter-annual variations were lower for size and Δ size than for mass and Δ mass, particularly
357 for younger age classes. Year as a discrete factor explained 11% and 58% (*i.e* variance
358 explained) of the inter-annual variations of juvenile size and mass, respectively. Inter-annual
359 variations remained constant for Δ size (juvenile: 8.7%, yearling: 9.7%, subadult: 9.4%)
360 whereas they decreased with age for Δ mass (juvenile: 44.2%, yearling: 34.4%, subadult:
361 17.4%, adult: 20.9%).

362 For each age class, there was a significant negative trend over the 22 years in size and
363 Δ size, while controlling for confounding variables (Table S6). Juvenile size as well as

364 yearling and subadult Δ size declined approximately by 3.9%, 4.4% and 3.8%, respectively.
365 Juvenile size decreased from 26.23 ± 0.01 (mean \pm SE) cm in 1992 to 25.20 ± 0.01 cm in
366 2012 (Fig. 1a). Despite a constant juvenile Δ size of 1.63 ± 0.01 , it decreased from 1.14 ± 0.01
367 to 1.09 ± 0.01 for yearlings and from 1.04 ± 0.01 to 1.00 ± 0.01 for subadults over the study
368 period (Fig. 1c). Our results from ANODEV supported an increased effect of long-term
369 temporal trend over age-classes. Long-term temporal trends explained 7.8% of the inter-
370 annual variations in juvenile size, and 2.4%, 24.9%, 36.4% for juvenile, yearling and subadult
371 Δ size, respectively. On the contrary, mass and Δ mass stayed constant between 1992 and 2012
372 (Table S6). Juvenile mass remained around 598.46 ± 1.02 g over the study period (Fig. 1b).
373 Except for an increase in subadult Δ mass from 1.05 ± 0.02 in 1992 to 1.11 ± 0.02 in 2012
374 (+5.7%), Δ mass was constant over time for all the other age classes (Fig. 1d). Long-term
375 temporal trends explained little of the inter-annual variation in juvenile mass (0.2%) and of
376 the inter-annual variation in Δ mass in all classes ($3.8 \pm 2.5\%$).

377

378 *Effects of environmental variables on size and Δ size*

379 Juvenile size (Fig. 2a) and both juvenile and yearling Δ size (Fig. 3a) were affected solely by
380 vegetation onset (Table 1). Juveniles became larger when vegetation onset was late and when
381 weaned early (mean size: 28.0 cm), but late vegetation onset was detrimental when juveniles
382 were weaned late (mean size: 22.4 cm, Fig. 2a). However, in years of early vegetation onset,
383 late weaning had less effect (mean size: 27.8 cm for early weaning vs. 25.9cm for late
384 weaning, Fig. 2a). Both juveniles and yearlings grew faster in years with earlier vegetation
385 onset, but this positive effect diminished with age (Fig. 3a, Table 1). While juvenile Δ size
386 increased by 0.031 (i.e., regression slope) for every standard deviation of vegetation onset
387 ($SD_{April\ NDVI} = 0.018$), it only increased by 0.014 for yearlings. Finally, subadult Δ size was not
388 affected by the vegetation onset.

389

390 *Effects of environmental variables on mass and Δ mass*

391 Contrary to juvenile size and Δ size, mass and Δ mass were affected not only by vegetation
392 onset during the spring but also by summer and winter conditions. Mass of juveniles (Fig. 2b)
393 and Δ mass of juveniles, yearlings and adults (Fig. 3b) were all affected by vegetation onset
394 (Table 1). As for size, juveniles became heavier when vegetation onset was late and when
395 weaned early (mean mass: 852.4 g), but late vegetation onset was detrimental when juveniles
396 were weaned late (mean mass: 365.2 g, Fig. 2b). However, in years of early vegetation onset,
397 late weaning had less effect (mean mass: 822.6 g for early weaning vs. 574.9 g for late
398 weaning, Fig. 2b). Similar to Δ size, Δ mass was influenced by vegetation onset in older
399 animals less than in juveniles and yearlings (Fig. 3b, Table 1). For every standard deviation
400 increase in vegetation onset ($SD_{April\ NDVI} = 0.018$), Δ mass increased by 0.21, 0.04, 0.02 and -
401 0.01 in juveniles, yearlings, adult subordinates and adult dominants, respectively (Fig. 3b).
402 Subadult Δ mass was not impacted by vegetation onset (Table 1), and, surprisingly, dominant
403 adults gained less mass with earlier vegetation onset compared to subordinate adults (Table 1,
404 Fig 3b).

405 In addition to vegetation onset, both summer condition index and winter snow depth affected
406 Δ mass of all age classes, except in subadults (Table 1, Fig. 3c,d). Δ mass of juveniles,
407 yearlings and adults increased more when the summer was mild and the winter was
408 characterized by a thin snow layer (Table 1). Subadult Δ mass has increased only in years with
409 thin snow layer (Table 1). Again, Δ mass response to both the summer condition index (Fig.
410 3c) and the winter snow depth (Fig. 3d) declined with age, although the differences among
411 age classes were stronger for summer than for winter variables. For every standard deviation
412 increase in summer condition index ($SD_{BGI} = 75.51$), Δ mass increased by 0.13, 0.03 and 0.01
413 in juveniles, yearlings and adults, while for every standard deviation increase in winter snow

414 depth ($SD_{snow\ depth} = 22.84\text{ cm}$), it increased by -0.05, -0.02, -0.02 and -0.01 in juveniles,
415 yearlings, subadults and adults, respectively. $\Delta mass$ was not affected by winter temperature in
416 any of the age classes.

417

418 *Relative influence of environmental variables*

419 From ANODEV, vegetation onset represented the most influential environmental variable
420 (Fig. 4). Within each age class, the relative amount of annual variation explained by
421 vegetation onset was similar for size and mass, and also for $\Delta size$ and $\Delta mass$. Summer
422 condition index and winter snow depth only accounted for inter-annual variations in $\Delta mass$.
423 Summer condition index explained a higher percentage of annual variation in juvenile and
424 yearling $\Delta mass$ than winter snow depth with lower evidence when individuals aged. Winter
425 snow depth explained a relatively small amount of these variations except in subadults.
426 Similar annual variations in adult $\Delta mass$ were explained by summer condition index and
427 winter snow depth.

428

429 *Components of phenotypic changes*

430 Using an age-structured Price equation, we decomposed the change in mean size and mass
431 into contributions from different life-history processes. Among individuals that survived, the
432 fluctuations observed for both size and mass were predominantly explained by age-specific
433 trait development accounted for by the growth term (GR: 49.3 % and 50% respectively; Fig.
434 5). Changes in the demographic composition accounted for more of the temporal fluctuations
435 in size than in mass. Demographic change due to aging (DCs) contributed more to the total
436 variation of both traits than the addition of new individuals (DCr). Inheritance-related term
437 (OMD) did not affect size variation and accounted for only a small fraction of the observed

438 change in mass (4.8%, Fig. 5). Selection terms (FS and VS) did not contribute to the observed
439 fluctuations either in size or in mass (Fig. 5).

440

441 **Discussion**

442 Our results provide an in-depth evaluation of the dynamics of size and mass in response to
443 environmental change using a hibernating mammal as the study species. Over the 22 years of
444 study, Alpine marmots' size decreased while mass stayed constant in each age class.
445 Moreover, initial size and Δ size responded only to inter-annual variations in spring conditions
446 whereas initial mass and Δ mass were further adjusted to summer and winter conditions.
447 Overall, phenotypic plasticity was the joint main origin of both traits dynamics.

448

449 *Differential dynamics of size and mass*

450 Over the study period, we found a slight decrease in juvenile size and yearling and subadult
451 Δ size, but not in juvenile Δ size. The absence of a temporal trend observed in juvenile Δ size is
452 possibly due to strong viability selection against smaller juveniles (Fig. S2). In contrast,
453 juvenile mass and subsequent Δ mass during juvenile, yearling and adult stages remained
454 constant. Concerning subadults, the positive trend observed in Δ mass might result from more
455 delayed dispersal in recent years. Indeed, subadult apparent survival increased over the
456 studied period while all other age classes' survival decreased or remained constant (Rézouki *et*
457 *al.*, unpublished data). Although body mass had no impact on the decision to disperse in
458 another Alpine population (Arnold, 1990a; Arnold, 1993), in our population, body mass was
459 influential on dispersal (Magnolon, 1999). Thus, recent environmental harshness at our study
460 site might have led subadults to stay longer in their natal territory in order to reach a critical
461 mass threshold for successful dispersal.

462 As a consequence of a smaller structural size associated with similar mass over the
463 study period, individuals were in better condition in recent years. In terms of energetics,
464 smaller structural size has two important consequences. First, it decreases per capita food
465 requirements and increases fasting resistance as individuals metabolize energy storage at a
466 lower size-specific rate, which in our case may be an advantage to overcome predictable
467 winter food shortage during the hibernation period (Millar *et al.*, 1990; Kooijman, 2000).
468 Second, decreasing size changes the sensitivity to the thermal environment, with smaller
469 individuals increasing their heat dissipation surface. Greater body heat loss is expected to be
470 beneficial during their active period to increase feeding time despite high ambient temperature
471 (Türk & Arnold, 1988) but should be detrimental during the hibernation period. An increased
472 cold-exposed body surface area should reduce hibernation efficiency through an increase in
473 energy expenditure to maintain a constant body temperature. But thermoregulatory costs
474 might be buffered by social thermoregulation through huddling (Arnold, 1990b; Arnold *et al.*,
475 1991; Gilbert *et al.*, 2010), which is beneficial in two ways. It increases thermal conduction
476 between close individuals and reduces the rate of cooling. Indeed, it prevents them against
477 further body temperature decrease during period of deep torpor when costly cyclic heat bursts
478 appear (Ortmann & Heldmaier, 2000; Ruf & Arnold, 2000).

479 The significant negative trend observed in size and Δ size is in line with the general
480 pattern evidenced by other studies examining size cline as a response to environmental change
481 (review in Sheridan *et al.*, 2011; Boutin *et al.*, 2014). On the contrary, the maintenance of
482 mass and Δ mass over the study period contrasts with this negative cline, but it reinforces the
483 fact that contemporary size responses are quite variable (*i.e* increasing or no change at all,
484 reviewed by Millien *et al.*, 2006; Gardner *et al.*, 2011; Yom-Tov *et al.*, 2011; Teplitsky *et al.*,
485 2014) and it highlights the contrasted dynamics between both traits. Despite the paucity of
486 long-term studies on wild birds and mammals evaluating the dynamics of both structural size

487 and mass (see Table 2), opposite cline between traits have also been reported in several other
488 endotherms species (eleven bird species and two mammal species, see details in Table 2). The
489 non-negligible number of studies showing different dynamics between structural size and
490 mass emphasizes the risk of looking at a single trait in trait-based population models
491 evaluating fitness consequences of morphological changes. In fact, among similar-weighted
492 individuals, smaller ones should present a better nutritional state than larger ones, which may
493 have direct consequences on individual life histories and ultimately fitness (Dobson, 1992;
494 Wauters *et al.*, 1995). Thus, studying one or the other trait can lead to ambiguous and
495 misleading conclusions. We should also note that studying their associations, using body
496 condition index, for example, can be inadequate to describe the potentially complex changes
497 in morphology that take place through time and can distort interpretation of the results. For
498 example, in roe deer fawns the synchronous responses of structural size and mass (fawns were
499 both lighter and smaller) led to a lack of response of body condition to a wide range of
500 changes in environmental conditions whereas their phenotypic quality was reduced (Toïgo *et*
501 *al.*, 2006).

502

503 *Different environmental drivers: a matter of sensitivity*

504 The phenotypic quality of Alpine marmots was favored by an early growing season resulting
505 from an early snowmelt with a moderately warm and rainy summer. Indeed, all traits
506 benefited from early access to resources in spring and in addition, Δ mass also responded to
507 summer and winter conditions with greater responses observed in early life, as expected both
508 from a theoretical and an empirical point of view (Forchhammer *et al.*, 2001; Gaillard &
509 Yoccoz, 2003). The strong responses of both morphological traits to spring phenology
510 reinforce the key role of nutritional condition during the green-up phase as the main driver of
511 phenotypic quality of mammalian herbivores (Inouye *et al.*, 2000; Pettorelli *et al.*, 2007;

512 Campbell *et al.*, 2013). To a lower extent than spring, hot and dry summer limited annual
513 Δ mass in juveniles, yearlings and adults probably as a result of lower quantity and quality of
514 food ingested, and restricted foraging time during the hot hours of the day (Türk & Arnold,
515 1988). Unexpectedly, winter severity plays a minor to no role on morphological variations.
516 Unsurprisingly, winter conditions did not affect Δ size as growth is greatly suppressed during
517 hibernation (Lyman *et al.*, 1956). Only snow depth showed a weak negative impact on Δ mass
518 in all age classes but no effect on weaning size or mass, whereas winter temperature did not
519 influence any traits. These counter-intuitive results might arise from social thermoregulation
520 that could have buffered the effect of winter conditions on individuals or from compensatory
521 effects during spring. Indeed, a catch-up might occur between the end of winter (April 15) and
522 the date of measurement (*i.e* July 14 for the juveniles and July 1 for other age class), hiding
523 the impact of winter severity.

524 Size-related traits showed weaker inter-annual variations than mass-related traits. At
525 the intra-annual scale, Δ size responded only to spring conditions whereas Δ mass was
526 constantly adjusted to environmental conditions throughout the year. The extreme variability
527 of mass compared to size indicates distinct sensitivity to environmental variables arising from
528 the different underlying physiological mechanisms driving energy allocation to these
529 functions. The longitudinal skeletal growth is driven by energy allocation to development
530 from birth to adulthood and mainly controlled by the growth hormone, the insulin-like growth
531 factor-1, glucocorticoids, and thyroid hormones interacting at the level of the
532 hypothalamopituitary axes (Robson *et al.*, 2002). Despite some exceptions of seasonal
533 reduction in braincase in small mammals (Dehnel, 1949; Pucek 1963), structural size remains
534 fixed at the adult stage in most endotherms, and its constituents cannot be utilized for energy
535 even under extreme starvation (Rizzoli, 2008). On the contrary, body mass is a composite of
536 structural mass, including bones, organs, skin, blood, skeletal muscle, and storage mass

537 (Wang et al., 1992; Fosbøl et al., 2015). It results from the fluctuations in energy intake and
538 expenditure (*i.e.* energy homeostasis) that is down regulated by complex nutrient, cytokines
539 and hormonal processes controlled by the whole central nervous system (Morton *et al.*, 2006).
540 If energy intake exceeds expenditure, the surplus is stored as fat, which can then fuel energy
541 demanding processes (*i.e.*, maintenance, growth or reproduction) during food shortage periods
542 (Piersma *et al.*, 1991). However, during a long fasting period, Δ mass might also result from
543 reduction in energy expensive tissues such as seasonal shrinkage of gastrointestinal tract in
544 alpine marmots during hibernation (Hume *et al.*, 2002) or garden warblers (*Sylvia borin*)
545 during migration (Hume & Biebach, 1996). Thus, it is not surprising that the energy allocation
546 trade-off between size and mass varied over season, life and environmental conditions. In
547 spring, energy is allocated to both constituents. However, later in the season, the irresponsive
548 growth to bad environmental conditions indicates priority of energy allocation to ensure
549 skeletal development, body fat probably being mobilized for it to compensate nutritional
550 deficiency as already observed in deer (Klein, 1964). However, in the case of favorable
551 summer environmental conditions, surplus nutrient are instead allocated to fattening, as
552 storage is crucial in marmots to overcome the fasting hibernation period.

553 In accordance with our study, other studies have shown different sensitivity to
554 environmental drivers between structural size and mass (Table 2). However, mass appears to
555 be sensitive to a larger number of environmental variables than size in only three other
556 species, namely great tits, river warblers and grizzly bears. In birds, similar environmental
557 drivers between both traits might not be surprising as they cannot store excess fat because
558 increased wing loading may decrease their flight performance and thus may increase their
559 susceptibility to predation (*i.e.* starvation-predation risk trade-off; Macleod *et al.*, 2005).
560 However, these results might be different when looking at migratory birds that can double
561 their mass due to different fuel loads and body composition (Lindström *et al.*, 1993).

562 Unfortunately, the studies reported in Table 2 were only on sedentary or pre-migratory birds
563 (except Kanuscack et al. 2004 that studied them on their migratory route). Concerning
564 mammals, we cannot draw any conclusion from only six studies among which four examined
565 at most two environmental drivers (Table 2). Moreover, given that the environmental drivers
566 chosen were mostly global change index processing both nutritional and thermal conditions
567 (Post *et al.*, 1997: North Atlantic Oscillation index; Toïgo *et al.*, 2006: spring and summer
568 Gausse Index; Rode *et al.*, 2010: availability of sea ice habitat; Yom-Tov *et al.*, 2010b: mean
569 annual temperature and number of days of ice coverage), distinct dynamics resulting from
570 different energetic pressure on size and mass cannot be disentangled.

571

572 *Phenotypic change: a plastic response*

573 The annual variation in both traits observed in this study was mainly triggered by their
574 development in early life stage. Although the ‘growth term’ from the age-structured Price
575 equation can include genetic components (Coulson *et al.*, 2008), the strong response we
576 observed to environmental conditions indicates mostly phenotypic plasticity that an animal
577 model type of approach should confirm. Our results add a sixth wild vertebrate species, in
578 addition to yellow-bellied marmots (Ozgul *et al.*, 2010), Soay sheep (Ozgul *et al.*, 2009), red-
579 billed gull (Teplitsky *et al.*, 2008), great tits (Husby *et al.*, 2011) and Siberian jays (Gienapp
580 *et al.*, 2014), that quantitatively demonstrates mostly ecological responses of morphological
581 traits to environmental variations. Mass variations of the Alpine marmot were subject to
582 similar relative contributions of plasticity and selection as the yellow-bellied marmots (Ozgul
583 *et al.*, 2010) despite harsher environmental conditions (*i.e* colder, prolonged winter with
584 extensive snow cover) reducing favorable foraging period in the Rocky Mountains (Armitage,
585 2014). Selection terms accounted for even less variation in our study population (0.96 % vs.
586 3% in yellow-bellied marmots). However, the paucity of evidence for genetic responses to

587 climate-mediated selection might arise from both methodological difficulties and/or biological
588 issues such as evolutionary time lags (Merilä, 2012). Our 22-year study period may have been
589 too short to detect a genetic response, as the rate of climate change might be too fast for
590 genetic adaptation to occur in species with long life spans as already observed in an emperor
591 penguin population (Forcada *et al.*, 2009; Jenouvrier *et al.*, 2009). It has also recently been
592 advocated that new phenotypes can first be induced by environmental conditions and then be
593 genetically assimilated, leading to genetic adaptation; as a result phenotypic plasticity is not
594 only a product but also a driver of genetic evolution (Kopp *et al.*, 2014).

595 The phenotypic plasticity observed in Alpine marmots does not appear adaptive
596 despite their wide ranged reaction norms (*i.e.*, phenotype as a function of an environmental
597 variable) showing their ability to withstand extreme environmental conditions. Indeed, recent
598 studies on this population showed a decline of individual performances over the past decades
599 with observed decreasing litter size, juvenile survival and family group size (Tafari *et al.*,
600 2013; Rézouki *et al.*, unpublished data). These results contrast with the abrupt increase in
601 population size of yellow-bellied marmots triggered by their mass shift (Ozgul *et al.*, 2010).
602 Although the structural size changes of yellow-bellied marmots remain unknown, the
603 different strategy between these species to maintain or increase their body condition by
604 decreasing structural size in Alpine marmots or increasing mass in yellow-bellied marmots
605 leads to drastic differences on their survival and reproductive rate. While both species are
606 closely related and respond plastically to environmental change, the strikingly different fitness
607 consequences highlight their different adaptive ability to face environmental change.

608

609 *Future directions and general implications*

610 Our research provides new insight for population modeling by drawing attention to
611 consideration of the differences between size and mass in response to the environment. We

612 provide further incentives to now disentangle causes and effects with environmental
613 manipulation to assess the underlying mechanisms of the different dynamics, and to quantify
614 the consequences of our measured changes on energy balance (Porter *et al.*, 2009; Gardner *et*
615 *al.*, 2011). To achieve further insight into the mechanisms driving population dynamics, the
616 challenge ahead will be to model the link between these traits and demographic performances.
617 The range of resilience conferred by plastic phenotypic compensations remains poorly
618 understood in wild species (Ghalambor *et al.*, 2007; Canale *et al.*, 2010) and might
619 dramatically differ between even closely related species as suggested for Alpine and yellow-
620 bellied marmots. The evaluation of the complex dynamics between traits and their distinct
621 sensitivity to environmental change will enhance our ability to assess whether or not
622 phenotypic plasticity could provide an adaptive response to environmental change.

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637

638 **References**

- 639 Allainé D (2000) Sociality, mating system and reproductive skew in marmots: evidence and
640 hypotheses. *Behavioural Processes*, **51**, 21-34.
- 641 Allainé D, Graziani L, Coulon J (1998) Postweaning mass gain in juvenile alpine marmots
642 *Marmota marmota*. *Oecologia*, **113**, 370-376.
- 643 Allainé D, Theuriau F (2004) Is there an optimal number of helpers in Alpine marmot family
644 groups? *Behavioral Ecology*, **15**, 916-924.
- 645 Armitage KB (2014) Marmots habitats in *Marmot Biology: Sociality, Individual Fitness, and*
646 *Population Dynamics*, Cambridge University Press, 43-56.

647 Arnold W (1990a) The evolution of marmot sociality: I. Why disperse late? Behavioral
648 Ecology and Sociobiology, **27**, 229-237.

649 Arnold W (1990b) The evolution of marmot sociality: II. Costs and benefits of joint
650 hibernation. Behavioral Ecology and Sociobiology, **27**, 239-246.

651 Arnold W (1993) Energetics of social hibernation. Life in the Cold: Ecological, Physiological
652 and Molecular Mechanisms, 65-80.

653 Arnold W, Dittami J (1997) Reproductive suppression in male alpine marmots. Animal
654 Behaviour, **53**, 53-66.

655 Arnold W, Heldmaier G, Ortmann S, Pohl H, Ruf T, Steinlechner S (1991) Ambient
656 temperatures in hibernacula and their energetic consequences for alpine marmots
657 (*Marmota marmota*). Journal of Thermal Biology, **16**, 223-226.

658 Ashton KG, Tracy MC, De Queiroz A (2000) Is Bergmann's rule valid for mammals? The
659 American Naturalist, **156**, 390-415.

660 Barton K, Barton MK (2015) Package 'MuMIn'. R package version, **1**, 18.

661 Basso B, De Simone L, Cammarano D et al. (2012) Evaluating responses to land degradation
662 mitigation measures in Southern Italy. International Journal of Environmental
663 Research, **6**, 367-380.

664 Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes.

665 Bel MC, Coulon J, Sreng L, Allaine D, Bagneres AG, Clement JL (1999) Social signals
666 involved in scent-marking behavior by cheek-rubbing in Alpine marmots (*Marmota*
667 *marmota*). Journal of Chemical Ecology, **25**, 2267-2283.

668 Beniston M (2006) Mountain weather and climate: a general overview and a focus on climatic
669 change in the Alps. Hydrobiologia, **562**, 3-16.

670 Bergmann C (1847) Uber die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse.
671 Gottinger Studien, **3**, 595-708.

672 Blackburn TM, Gaston KJ (1994) Animal body size distributions: patterns, mechanisms and
673 implications. *Trends in Ecology & Evolution*, **9**, 471-474.

674 Boutin S, Lane JE (2014) Climate change and mammals: evolutionary versus plastic
675 responses. *Evolutionary Applications*, **7**, 29-41.

676 Büntgen U, Liebhold A, Jenny H *et al.* (2014) European springtime temperature synchronises
677 ibex horn growth across the eastern Swiss Alps. *Ecology Letters*, **17**, 303-313.

678 Burnham KP, Anderson DR (2002) *Model selection and multi-model inference: a practical*
679 *information-theoretic approach*, Berlin, Germany, Springer.

680 Calder WA (1984) *Size, function, and life history*, Courier Corporation.

681 Campbell RD, Newman C, Macdonald DW, Rosell F (2013) Proximate weather patterns and
682 spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and
683 reproductive success: the implications of climate change and topography. *Global*
684 *Change Biology*, **19**, 1311-1324.

685 Canale CI, Henry PY (2010) Adaptive phenotypic plasticity and resilience of vertebrates to
686 increasing climatic unpredictability. *Climate Research*, **43**, 135-147.

687 Cohas A, Yoccoz NG, Bonenfant C *et al.* (2008) The genetic similarity between pair members
688 influences the frequency of extrapair paternity in alpine marmots. *Animal Behaviour*,
689 **76**, 87-95.

690 Cooch E, Lank D, Rockwell R, Cooke F (1991) Long-term decline in body size in a snow
691 goose population: evidence of environmental degradation? *The Journal of Animal*
692 *Ecology*, 483-496.

693 Coulson T, Tuljapurkar S (2008) The Dynamics of a Quantitative Trait in an Age-Structured
694 Population Living in a Variable Environment. *The American Naturalist*, **172**, 599-612.

695 Dajoz R (1973) *Précis d'écologie*, Gauthier Villars.

696 Davis EB (2005) Comparison of climate space and phylogeny of *Marmota* (Mammalia :
697 Rodentia) indicates a connection between evolutionary history and climate preference.
698 Proceedings of the Royal Society B-Biological Sciences, **272**, 519-526.

699 Dehnel A (1949) Studies on the genus *Sorex* L. Annales of the university of M. Curie-
700 Sklodowska, Section C, **4**, 17-102.

701 Dejong G (1995) Phenotypic plasticity as a product of selection in a variable environment
702 American Naturalist, **145**, 493-512.

703 Dickey M, Gauthier G, Cadieux M-C (2008) Climatic effects on the breeding phenology and
704 reproductive success of an arctic-nesting goose species. Global Change Biology, **14**,
705 1973-1985.

706 Dobson FS (1992) Body mass, structural size, and life-history patterns of the Columbian
707 ground squirrel. American Naturalist, 109-125.

708 Eastman LM, Morelli TL, Rowe KC, Conroy CJ, Moritz C (2012) Size increase in high
709 elevation ground squirrels over the last century. Global Change Biology, **18**, 1499-
710 1508.

711 Engler R, Randin CF, Thuiller W *et al.* (2011) 21st century climate change threatens
712 mountain flora unequally across Europe. Global Change Biology, **17**, 2330-2341.

713 Farand E, Allainé D, Coulon J (2002) Variation in survival rates for the alpine marmot
714 (*Marmota marmota*): effects of sex, age, year, and climatic factors. Canadian Journal
715 of Zoology-Revue Canadienne De Zoologie, **80**, 342-349.

716 Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean.
717 Global Change Biology, **15**, 1618-1630.

718 Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD (2001) Climate and population
719 density induce long-term cohort variation in a northern ungulate. Journal of Animal
720 Ecology, **70**, 721-729.

721 Fosbøl MØ, Zerahn B (2015) Contemporary methods of body composition measurement.
722 Clinical Physiology and Functional Imaging, **35**, 81-97.

723 Fox J (2003) Effect displays in R for generalised linear models. Journal of Statistical
724 Software, **8**, 1-27.

725 Fox J, Hong J (2009) Effect displays in R for multinomial and proportional-odds logit
726 models: Extensions to the effects package. Journal of Statistical Software, **32**, 1-24.

727 Gaillard, J.-M. et al. (1997) Early survival in roe deer: causes and consequences of cohort
728 variation in two contrasted populations. Oecologia, **112**, 502-513.

729 Gaillard J-M, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of
730 environmental canalization? Ecology, **84**, 3294-3306.

731 Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third
732 universal response to warming? Trends in Ecology & Evolution, **26**, 285-291.

733 Garel, M. et al. (2004) The effects of a severe drought on mouflon lamb survival. -
734 Proceedings of the Royal Society of London. Series B: Biological Sciences, **271**, 471-
735 473.

736 Ghalambor CK, Mckay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive
737 phenotypic plasticity and the potential for contemporary adaptation in new
738 environments. Functional Ecology, **21**, 394-407.

739 Gienapp P, Merilä J (2014) Disentangling plastic and genetic changes in body mass of
740 Siberian jays. Journal of Evolutionary Biology, **27**, 1849-1858.

741 Gienapp P, Teplitsky C, Alho JS, Mills JA, Merila J (2008) Climate change and evolution:
742 disentangling environmental and genetic responses. Molecular Ecology, **17**, 167-178.

743 Gilbert C, Mcafferty D, Le Maho Y, Martrette JM, Giroud S, Blanc S, Ancel A (2010) One
744 for all and all for one: the energetic benefits of huddling in endotherms. Biological
745 Reviews, **85**, 545-569.

746 Green AJ (2001) Mass/length residuals: Measures of body condition or generators of spurious
747 results? Ecology, **82**, 1473-1483.

748 Grosbois V, Gimenez O, Gaillard JM *et al.* (2008) Assessing the impact of climate variation
749 on survival in vertebrate populations. Biological Reviews, **83**, 357-399.

750 Guillemain M, Mondain-Monval J-Y, Johnson AR, Simon G (2005) Long-term climatic trend
751 and body size variation in teal *Anas crecca*. Wildlife Biology, **11**, 81-88.

752 Hackländer K, Möstl E, Arnold W (2003) Reproductive suppression in female Alpine
753 marmots, *Marmota marmota*. Animal Behaviour, **65**, 1133-1140.

754 Hamel S, Garel M, Festa-Bianchet M, Gaillard JM, Côté SD (2009) Spring Normalized
755 Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal
756 crude protein in mountain ungulates. Journal of Applied Ecology, **46**, 582-589.

757 Heldmaier G (1989) Seasonal acclimatization of energy requirements in mammals: functional
758 significance of body weight control, hypothermia, torpor and hibernation. Energy
759 transformations in cells and organisms. Thieme, Stuttgart, 130-139.

760 Hembeck H (1958) Zum Paarungsverhalten der Murmeltiere. Z Jagdwiss, **4**, 40-41.

761 Hersteinsson P, Yom-Tov Y, Geffen E (2009) Effect of Sub-Polar Gyre, North Atlantic
762 Oscillation and ambient temperature on size and abundance in the Icelandic Arctic
763 fox. Global Change Biology, **15**, 1423-1433.

764 Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature, **470**,
765 479-485.

766 Hou C, Zuo W, Moses ME, Woodruff WH, Brown JH, West GB (2008) Energy uptake and
767 allocation during ontogeny. Science, **322**, 736-739.

768 Huey RB, Kearney MR, Krockenberger A, Holtum JaM, Jess M, Williams SE (2012)
769 Predicting organismal vulnerability to climate warming: roles of behaviour,

770 physiology and adaptation. Philosophical Transactions of the Royal Society B-
771 Biological Sciences, **367**, 1665-1679.

772 Hume I, Biebach H (1996) Digestive tract function in the long-distance migratory garden
773 warbler, *Sylvia borin*. Journal of Comparative Physiology B, **166**, 388-395.

774 Hume I, Beiglböck C, Ruf T, Frey-Roos F, Bruns U, Arnold W (2002) Seasonal changes in
775 morphology and function of the gastrointestinal tract of free-living alpine marmots
776 (*Marmota marmota*). Journal of Comparative Physiology B: Biochemical, Systemic,
777 and Environmental Physiology, **172**, 197-207.

778 Husby A, Hille SM, Visser ME (2011) Testing mechanisms of Bergmann's rule: phenotypic
779 decline but no genetic change in body size in three passerine bird populations. The
780 American Naturalist, **178**, 202-213.

781 Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal
782 migrants and hibernating species. Proceedings of the National Academy of Sciences of
783 the United States of America, **97**, 1630-1633.

784 Janz KF (2004) *Growth, maturation, and physical activity, 2nd edition*. American Journal of
785 Human Biology: The Official Journal of the Human Biology Council.

786 Jenouvrier S, Caswell H, Barbraud C, Holland M, Ströve J, Weimerskirch H (2009)
787 Demographic models and IPCC climate projections predict the decline of an emperor
788 penguin population. Proceedings of the National Academy of Sciences, **106**, 1844-
789 1847.

790 Kaňuščák P, Hromada M, Tryjanowski P, Sparks T (2004) Does climate at different scales
791 influence the phenology and phenotype of the River Warbler *Locustella fluviatilis*?
792 Oecologia, **141**, 158-163.

793 Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and
794 spatial data to predict species' ranges. Ecology Letters, **12**, 334-350.

795 Keller F, Goyette S, Beniston M (2005) Sensitivity analysis of snow cover to climate change
796 scenarios and their impact on plant habitats in alpine terrain. *Climatic Change*, **72**,
797 299-319.

798 Klein DR (1964) Range-related differences in growth of deer reflected in skeletal ratios.
799 *Journal of Mammalogy*, 226-235.

800 Kooijman SaLM (2000) *Dynamic energy and mass budgets in biological systems*, Cambridge
801 University Press.

802 Kopp M, Matuszewski S (2014) Rapid evolution of quantitative traits: theoretical
803 perspectives. *Evolutionary Applications*, **7**, 169-191.

804 Körtner G, Heldmaier G (1995) Body weight cycles and energy balance in the alpine marmot
805 (*Marmota marmota*). *Physiological Zoology*, 149-163.

806 Lardy S, Cohas A, Desouhant E, Tafani M, Allaine D (2012) Paternity and dominance loss in
807 male breeders: the cost of helpers in a cooperatively breeding mammal. *Plos One*, **7**,
808 e29508.

809 Lenihan C, Van Vuren D (1996) Growth and survival of juvenile yellow-bellied marmots
810 (*Marmota flaviventris*). *Canadian Journal of Zoology*, **74**, 297-302.

811 Lindström A, Piersma T (1993) Mass changes in migrating birds: the evidence for fat and
812 protein storage re-examined. *Ibis*, **135**, 70-78.

813 Lyman CP, Chatfield PO (1956) Physiology of hibernation in mammals. *The Physiology of*
814 *Induced Hypothermia*, **1**, 80-122.

815 Macleod R, Barnett P, Clark J, Cresswell W (2005) Body mass change strategies in blackbirds
816 *Turdus merula*: the starvation–predation risk trade-off. *Journal of Animal Ecology*, **74**,
817 292-302.

818 Magnolon S (1999) La dispersion natale chez la marmotte alpine (*Marmota marmota*).
819 Modalités et effets de quelques facteurs proximaux. Thèse de Doctorat. Université
820 Francois Rabelais, Tours.

821 McNab BK (1999) On the comparative ecological and evolutionary significance of total and
822 mass-specific rates of metabolism. *Physiological and Biochemical Zoology*, **72**, 642-
823 644.

824 Maiorano L, Amori G, Capula M *et al.* (2013) Threats from climate change to terrestrial
825 vertebrate hotspots in Europe. *Plos One*, **8**, e74989.

826 Marroig G, Cheverud J (2010) Size as a line of least resistance II: Direct selection on size or
827 correlated response due to constraints? *Evolution*, **64**, 1470-1488.

828 McMahon SM, Harrison SP, Armbruster WS *et al.* (2011) Improving assessment and
829 modelling of climate change impacts on global terrestrial biodiversity. *Trends in*
830 *Ecology & Evolution*, **26**, 249-259.

831 McNab BK (2010) Geographic and temporal correlations of mammalian size reconsidered: a
832 resource rule. *Oecologia*, **164**, 13-23.

833 Meiri S (2011) Bergmann's Rule—what's in a name? *Global Ecology and Biogeography*, **20**,
834 203-207.

835 Merilä J (2012) Evolution in response to climate change: in pursuit of the missing evidence.
836 *Bioessays*, **34**, 811-818.

837 Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the
838 problem and the evidence. *Evolutionary Applications*, **7**, 1-14.

839 Michener DR (1974) Annual cycle of activity and weight changes in Richardson's ground
840 squirrel, *Spermophilus richardsonii*. *Canadian Field-Naturalist*, **88**, 409-413.

841 Millar J, Hickling G (1990) Fasting endurance and the evolution of mammalian body size.
842 *Functional Ecology*, 5-12.

843 Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom-Tov Y (2006) Ecotypic variation
844 in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**, 853-
845 869.

846 Monaghan P (2008) Early growth conditions, phenotypic development and environmental
847 change. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**,
848 1635-1645.

849 Moreno-Rueda G, Rivas JM (2007) Recent changes in allometric relationships among
850 morphological traits in the dipper (*Cinclus cinclus*). *Journal of Ornithology*, **148**, 489-
851 494.

852 Morton G, Cummings D, Baskin D, Barsh G, Schwartz M (2006) Central nervous system
853 control of food intake and body weight. *Nature*, **443**, 289-295.

854 Müller-Using D (1957) Die Paarungsbiologie des Murmeltieres. *Z Jagdwiss*, **3**, 24-28.

855 Nielsen SE, Cattet MR, Boulanger J, Cranston J, Mcdermid GJ, Shafer AB, Stenhouse GB
856 (2013) Environmental, biological and anthropogenic effects on grizzly bear body size:
857 temporal and spatial considerations. *BMC Ecology*, **13**, 31.

858 Ortman S, Heldmaier G (2000) Regulation of body temperature and energy requirements of
859 hibernating Alpine marmots (*Marmota marmota*). *American Journal of Physiology-
860 Regulatory, Integrative and Comparative Physiology*, **278**, R698-R704.

861 Ozgul A, Bateman AW, English S, Coulson T, Clutton-Brock TH (2014) Linking body mass
862 and group dynamics in an obligate cooperative breeder. *Journal of Animal Ecology*,
863 **83**, 1357-1366.

864 Ozgul A, Childs DZ, Oli MK *et al.* (2010) Coupled dynamics of body mass and population
865 growth in response to environmental change. *Nature*, **466**, 482-485.

866 Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T (2009)
867 The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda. *Science*,
868 **325**, 464-467.

869 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual*
870 *Review of Ecology Evolution and Systematics*, **37**, 637-669.

871 Peig J, Green AJ (2010) The paradigm of body condition: a critical reappraisal of current
872 methods based on mass and length. *Functional Ecology*, **24**, 1323-1332.

873 Perrin C, Allainé D, Leberre M (1993) Socio-spatial organization and activity distribution of
874 the Alpine marmot (*Marmota marmota*) - preliminary results. *Ethology*, **93**, 21-30.

875 Pettorelli N, Gaillard J-M, Van Laere G *et al.* (2002) Variations in adult body mass in roe
876 deer: the effects of population density at birth and of habitat quality. *Proceedings of*
877 *the Royal Society of London. Series B: Biological Sciences*, **269**, 747-753.

878 Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the
879 satellite-derived NDVI to assess ecological responses to environmental change.
880 *Trends in Ecology & Evolution*, **20**, 503-510.

881 Pettorelli N, Pelletier F, Hardenberg AV, Festa-Bianchet M, Côté SD (2007) Early onset of
882 vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates.
883 *Ecology*, **88**, 381-390.

884 Piersma T, Davidson NC (1991) Confusions of mass and size. *The Auk*, 441-443.

885 Porter WP, Kearney M (2009) Size, shape, and the thermal niche of endotherms. *Proceedings*
886 *of the National Academy of Sciences*, **106**, 19666-19672.

887 Post E, Stenseth NC, Langvatn R, Fromentin J-M (1997) Global climate change and
888 phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of*
889 *London. Series B: Biological Sciences*, **264**, 1317-1324.

890 Psenner H (1957) Neues vom Murmeltier, *Marmota m. marmota* (Linne, 1758). Säugetierk
891 Mitt, **5**, 4-10.

892 Pucek Z (1963) Seasonal changes in the braincase of some representatives of the genus *Sorex*
893 from the Palearctic. *Journal of Mammalogy*, **44**, 523-536.

894 R Core Team (2014). R: A language and environment for statistical computing. R Foundation
895 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

896 Rioux Paquette S, Pelletier F, Garant D, Bélisle M (2014) Severe recent decrease of adult
897 body mass in a declining insectivorous bird population. *Proceedings of the Royal*
898 *Society B: Biological Sciences*, **281**, 20140649.

899 Rizzoli R (2008) Nutrition: its role in bone health. *Best Practice & Research Clinical*
900 *Endocrinology & Metabolism*, **22**, 813-829.

901 Robson H, Siebler T, Shalet SM, Williams GR (2002) Interactions between GH, IGF-I,
902 glucocorticoids, and thyroid hormones during skeletal growth. *Pediatric research*, **52**,
903 137-147.

904 Roche EA, Brown MB, Brown CR (2014) The Effect of Weather on Morphometric Traits of
905 Juvenile Cliff Swallows. *Prairie Naturalist*, **46**, 2.

906 Rode KD, Amstrup SC, Regehr EV (2010) Reduced body size and cub recruitment in polar
907 bears associated with sea ice decline. *Ecological Applications*, **20**, 768-782.

908 Ruf T, Arnold W (2000) Mechanisms of social thermoregulation in hibernating alpine
909 marmots (*Marmota marmota*). *Life in the Cold*. Berlin: Springer, 81-94.

910 Salewski V, Hochachka WM, Fiedler W (2010) Global warming and Bergmann's rule: do
911 central European passerines adjust their body size to rising temperatures? *Oecologia*,
912 **162**, 247-260.

913 Schamber JL, Esler D, Flint PL (2009) Evaluating the validity of using unverified indices of
914 body condition. *Journal of Avian Biology*, **40**, 49-56.

915 Schmidt-Nielsen K (1984) *Scaling: why is animal size so important?*, Cambridge University
916 Press.

917 Seebacher F, Franklin CE (2012) Determining environmental causes of biological effects: the
918 need for a mechanistic physiological dimension in conservation biology. *Philosophical
919 Transactions of the Royal Society B-Biological Sciences*, **367**, 1607-1614.

920 Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate
921 change. *Nature Climate Change*, **1**, 401-406.

922 Skalski JR (1996) Regression of abundance estimates from mark recapture surveys against
923 environmental covariates. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**,
924 196-204.

925 Smith FA, Browning H, Shepherd UL (1998) The influence of climate change on the body
926 mass of woodrats *Neotoma* in an arid region of New Mexico, USA. *Ecography*, **21**,
927 140-148.

928 Smith FA, Lyons SK (2013) *Animal body size: linking pattern and process across space,
929 time, and taxonomic group*, University of Chicago Press.

930 Somero GN (2012) The Physiology of Global Change: Linking Patterns to Mechanisms.
931 *Annual Review of Marine Science*, **4**, 39-61.

932 Tafani M, Cohas A, Bonenfant C, Gaillard JM, Allainé D (2013) Decreasing litter size of
933 marmots over time: a life history response to climate change? *Ecology*, **94**, 580-586.

934 Teplitsky C, Millien V (2014) Climate warming and Bergmann's rule through time: is there
935 any evidence? *Evolutionary Applications*, **7**, 156-168.

936 Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merila J (2008) Bergmann's rule and climate
937 change revisited: Disentangling environmental and genetic responses in a wild bird
938 population. *Proceedings of the National Academy of Sciences of the United States of
939 America*, **105**, 13492-13496.

940 Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the
941 European Alps: A review. *Climatic Change*, **50**, 77-109.

942 Toïgo C, Gaillard JM, Van Laere G, Hewison M, Morellet N (2006) How does environmental
943 variation influence body mass, body size, and body condition? Roe deer as a case
944 study. *Ecography*, **29**, 301-308.

945 Türk A, Arnold W (1988) Thermoregulation as a limit to habitat use in alpine marmots
946 (*Marmota marmota*). *Oecologia*, **76**, 544-548.

947 Wang Z-M, Pierson R, Heymsfield SB (1992) The five-level model: a new approach to
948 organizing body-composition research. *The American Journal of Clinical Nutrition*,
949 **56**, 19-28.

950 Wauters L, Dhondt AA (1995) Lifetime reproductive success and its correlates in female
951 Eurasian red squirrels. *Oikos*, 402-410.

952 Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an Integrated
953 Framework for Assessing the Vulnerability of Species to Climate Change. *PLoS*
954 *Biology*, **6**, 2621-2626.

955 Yoccoz NG, Delestrade A, Loison A (2010) Impact of climatic change on alpine ecosystems:
956 inference and prediction. *Journal of Alpine Research-Revue de géographie alpine*, no
957 98-4.

958 Yom-Tov Y (2001) Global warming and body mass decline in Israeli passerine birds.
959 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 947-
960 952.

961 Yom-Tov Y, Geffen E (2011) Recent spatial and temporal changes in body size of terrestrial
962 vertebrates: probable causes and pitfalls. *Biological Reviews*, **86**, 531-541.

963 Yom-Tov Y, Leader N, Yom-Tov S, Baagøe HJ (2010a) Temperature trends and recent
964 decline in body size of the stone marten *Martes foina* in Denmark. Mammalian
965 Biology-Zeitschrift fur Saugetierkunde, **75**, 146-150.

966 Yom-Tov Y, Roos A, Mortensen P, Wiig Ø, Yom-Tov S, Heggberget TM (2010b) Recent
967 changes in body size of the Eurasian otter *Lutra lutra* in Sweden. *Ambio*, **39**, 496-503.

968 Yom-Tov Y, Yom-Tov J (2005) Global warming, Bergmann's rule and body size in the
969 masked shrew *Sorex cinereus* Kerr in Alaska. *Journal of Animal Ecology*, **74**, 803-
970 808.

971 Yom-Tov Y, Yom-Tov S (2004) Climatic change and body size in two species of Japanese
972 rodents. *Biological Journal of the Linnean Society*, **82**, 263-267.

973 Yom-Tov Y, Yom-Tov S, Angerbjorn A (2010c) Body size of the weasel *Mustela nivalis* and
974 the stoat *M. erminea* in Sweden. *Mammalian Biology-Zeitschrift fur Saugetierkunde*,
975 **75**, 420-426.

976

977 **Supporting Information**

978 Additional Supporting Information may be found in the online version of this article:

979 **Appendix S1.** Intra-annual variation in size and mass.

980 **Fig. S1.** Timeline of size and mass estimates shown on the life cycle of alpine marmots.

981 **Table S1.** Age-specific linear mixed models describing inter-annual variations and long-term
982 temporal trends.

983 **Table S2.** Age-specific linear mixed models describing the effect of environmental variables.

984 **Table S3.** Correlation matrix among environmental variables.

985 **Table S4.** Variance inflation-factors among environmental variables.

986 **Table S5.** Model selection of the full set of models for all alternatives concerning
987 environmental variables.

988 **Table S6.** Age-specific linear mixed models testing for long-term linear temporal trend.

989 **Table S7.** Age-specific linear mixed models testing for environmental effects.

990 **Fig S2.** Age-specific viability selection contributions to changes in the mean value of size.

991

992 **FIGURES AND TABLES CAPTION**

993 **Fig. 1** Temporal changes in stage specific size, mass, Δ size and Δ mass. Yearly variation in (a)
994 size, (b) mass, (c) Δ size and (d) Δ mass of juvenile (), yearling (), subadult
995 (), subordinate adult () and dominant adult () Alpine marmots at La Grande
996 Sassièrè (French Alps) from 1992 to 2012. Solid lines represent model predictions and dashed
997 lines their associated standard error. Symbols represent model residuals after controlling for
998 confounding variables (for details see the Materials and methods section).

999

1000 **Fig. 2** Vegetation onset and date of weaning effects on (a) size and (b) mass of juveniles. The
1001 grey surface represents model predictions. Dots represent model residuals after controlling for
1002 confounding variables (for details see the Materials and methods section). Black dots are
1003 above the predicted values and white dots below the predicted values.

1004 **Fig. 3** Environmental factors driving stage specific Δ size and Δ mass. Effects of (a) vegetation
1005 onset on Δ size, and of (b) vegetation onset, (c) summer condition index, (d) winter snow depth
1006 on Δ mass of juvenile (), yearling (), subadult (), adult subordinate (),
1007 adult dominant () or both subordinate adult and dominant adult () Alpine marmots at
1008 La Grande Sassièrè (French Alps) from 1992 to 2012. Solid lines represent model predictions
1009 and dashed lines represent their associated standard error. Symbols represent the residuals after
1010 controlling for confounding variables (for details see the Materials and methods section).
1011 Environmental variables were mean-centered and standardized.

1012

1013 **Fig. 4** Relative influence of environmental variables. Proportion of the variance in size, mass,
1014 Δ size and Δ mass explained by significant environmental variables.

1015

1016 **Fig. 5** Components of phenotypic changes. Percentage contribution of the different terms to
1017 the observed total variation in size and mass. The change in the mean value of both traits were
1018 decomposed into contributions from age-specific trait development (Gr), changes in
1019 demographic structure caused by age-specific survival rates (DCs) or caused by age-specific
1020 reproduction (DCr), offspring-mother difference (OMD), age-specific viability selection (VS)
1021 and age-specific fertility selection (FS).

1022

1023 **Table 1** Environmental effects in size, mass and Δ size and Δ mass. Statistically significant
1024 environmental effects in (a) size and mass in juvenile and on Δ size and Δ mass in (b) juvenile,
1025 (c) yearling, (d) subadult and (e) adult Alpine marmots at La Grande Sassièrè (French Alps)
1026 from 1992 to 2012. We modeled Δ size and Δ mass conditional on initial size and mass,
1027 respectively. All size and mass measurements in the response variables and model terms were
1028 log-transformed. We controlled for confounding variables (not shown here, see Table S7 for
1029 details) and we included as additive random effects on the intercept, territory in all models
1030 and marmot identity in the adult models. Parameter estimates and their associated standard
1031 errors (SE) were obtained from the best model based on the Akaike Information Criterion for
1032 small sample size (AICc) (see Table S5). Baseline intercepts are established for dominants in
1033 the adult model.

1034

1035 **Table 2** A synopsis of long-term studies looking at both size and mass dynamics in wild birds
1036 and mammals. We excluded studies reporting changes from museums specimens. Temporal

1037 trends in bold indicates opposite trends between size and mass. For environmental drivers, we
1038 show the number of environmental factors that had a significant impact on size and mass over
1039 how many have been tested. Bold numbers show studies demonstrating that mass and size
1040 were driven by a different number of environmental variables. * indicates studies where mass
1041 was adjusted to a larger number of environmental variables than size.