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Causes and consequences of the Yellow-Bellied Marmot's body mass shift in the last half century.

Background: Natural selection shapes an organism's phenotype to optimize its fitness within its environment (Darwin 1859). When environmental conditions change, species typically respond in one of two ways: disperse or adapt (Gienapp and Brommer 2014a). Adaptation occurs through **phenotypic plasticity**, where a genotype can express different phenotypes depending on environmental conditions, or **microevolution**, which involves shifts in allele frequencies within the population. While plasticity often provides a short-term solution, microevolution drives more permanent changes. Understanding how much each mechanism contributes to phenotypic changes is critical, especially in the context of climate change, where the consequences for populations could vary dramatically over time.

It is also crucial to understand that a Life-History Trait (LHT, i.e. a phenotypic trait that affects an indvidual's survival and reproduction, Partridge and Harvey 1988) cannot evolve alone. Coevolution must be take into account, and there is a growing need to conduct more multivariate analyses to understand evolutionary potential and identify potential constraints. This is crucial to understand how a population can cope with environmental changes, particularly, again, in the context of climate change (Gienapp and Brommer 2014b; Teplitsky et al. 2014).

Researchers have suggested that global warming could lead to a universal decrease in body size, in line with Bergmann's rule on heat dissipation (Bergmann 1847; Daufresne et al. 2009). However, long-term evidence supporting this pattern is scarce (Gardner et al. 2011), and studies at higher latitudes have regularly produced contradictory findings (Guillemain et al. 2010; Sheridan and Bickford 2011; Yom-Tov et al. 2008). This contradictory pattern has been observed in Yellow-Bellied Marmots (YBM), Marmota flaviventris. A wild population in the Upper East River valley, Colorado, USA is the subject of the second longest-running wild mammal population studies in the world. It is also one of the most complete, with a tremendous quantity and variety of collected data (more details in Armitage 2014). We have extensive data about marmot's life cycle, morphology, genetics, environment, etc. which allows for comprehensive analyses. In this system, we have observed an increase in body mass in the last decades (1970s - 2010s). Initially, this shift was attributed to phenotypic plasticity resulting from milder environmental conditions and longer active season (Ozgul et al. 2010).

However, recent work has raised question about the use of Integral Projection Model (IPMs) in making evolutionary inferences (Chevin 2015; Janeiro et al. 2017). I studied this case, using quantitative genetic analysis, especially the Animal Model (in a Bayesian framework: MCMCglmm, Hadfield 2010), which is a specific kind of mixed model which uses a random individual effect linked with the population pedigree (i.e. parental links between each individual of the population) to decompose the phenotypic variance and estimates it genetic part (Kruuk 2004). My preliminary research reveals a strong evolutionary signal alongside phenotypic plasticity. While the lengthening of the active season provides an ecological explanation for the observed plasticity, it does not account for the evolutionary changes. A longer active season should reduce selective pressure for larger body mass. Thus, the aim of my PhD is to rethink the evolutionary drivers behind the observed body mass increase in the last half-century in a wild YBM population. Then study the consequences of significant change in a LHT such as body mass in a hibernating species.

Research Questions (RQ) and Methods: I will address two main research questions, each divided into several hypotheses with corresponding methodologies.

RQ1: What are the causes of the observed body mass evolution?

• **Hypothesis 1**: Punctual extreme weather events have acted as selection bottlenecks, favouring heavier individuals in the population.

- Methodology 1: I will analyze extreme weather events occurrences at the study sites and investigate their link with population fluctuations and mean body mass' genetic values over the study period.
- **Hypothesis 2**: Drought events, which have become more frequent with global warming, increase the proportion of dry vegetation, enhancing selection for larger individuals able consume a more fibrous diet due to longer Mean Retention Time (MRT) (Armitage 2014).
 - Methodology 2: I will study marmots' diet composition over the years to evaluate changes in vegetation quality and selection.
- **Hypothesis 3**: Larger individuals will be favoured by natural selection as they are better able to fend off smaller predators such as Long-Tailed Weasels (*Mustela frenata*) and American Marten (*Martes americana*) (Armitage 2014).
 - Methodology 3: I will examine predators population dynamics and species composition and compare that to the recorded causes of marmot mortality over the study period.

RQ2: What are the short- and long-term consequences of this shift in a Life-History Trait (LHT)?

- **Hypothesis 4**: A significant shift in body mass, combined with environmental changes, will alter the life cycle of this hibernating species.
 - **Methodology 4**: I will investigate changes in the active season/hibernation length balance and examine potential correlations with body mass and environmental factors.
- Hypothesis 5: A shift in body condition will result in behavioural changes at the individual level.
 - Methodology 5: I will assess changes in individual behavior by analysing boldness data collected through Flight Initiation Distance (FID) experiments over the study period and test for link with body mass.

Significance and Impact: This research uses one of the most extensive natural population databases in the world to deepen our understanding of the genotype-phenotype-environment relationship. It will provide crucial insights into how wild populations adapt to changing environments. The project aims to illustrate the multimodel nature of both causes and consequences of this phenotipic shift (i.e. body mass increase), as we anticipate that no single hypothesis will fully explqin the observed changes. Instead, we expect that each hypothesis will account for part of the process, either complementing or conflicting with one another. These findings will contribute valuable knowledge to the field of conservation biology, helping shape more effective conservation policies in the context of global climate change.

References

- Armitage, K. B. (2014), "Marmot biology." https://doi.org/10.1017/cbo9781107284272.
- Bergmann, C. (1847), "About the relationships between heat conservation and body size of animals," *Goett Stud*, 1.
- Chevin, L. (2015), "Evolution of adult size depends on genetic variance in growth trajectories: A comment on analyses of evolutionary dynamics using integral projection models," *Methods in Ecology and Evolution*, (S. Ramula, ed.), 6, 981–986. https://doi.org/10.1111/2041-210X.12389.
- Darwin, C. (1859), The Origin of Species: By Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, Cambridge University Press. https://doi.org/10.1017/CBO9780511694295.
- Daufresne, M., Lengfellner, K., and Sommer, U. (2009), "Global warming benefits the small in aquatic ecosystems," *Proceedings of the National Academy of Sciences*, 106, 12788–12793. https://doi.org/10.1073/pnas.0902080106.
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. (2011), "Declining body size: A third universal response to warming?" *Trends in Ecology & Evolution*, 26, 285–291. https://doi.org/10.1016/j.tree.2011.03.005.
- Gienapp, P., and Brommer, J. E. (2014a), "Evolutionary dynamics in response to climate change," in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 254–274. https://doi.org/10.1093/acprof:oso/9780199674237.003.0015.
- Gienapp, P., and Brommer, J. E. (2014b), "Evolutionary dynamics in response to climate change," in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 254–274. https://doi.org/10.1093/acprof:oso/9780199674237.003.0015.
- Guillemain, M., Elmberg, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J., and Simon, G. (2010), "Wintering French Mallard and Teal Are Heavier and in Better Body Condition than 30 Years Ago: Effects of a Changing Environment?" *AMBIO*, 39, 170–180. https://doi.org/10.1007/s13280-010-0020-9.
- Hadfield, J. D. (2010), "MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm r Package," Journal of Statistical Software, 33. https://doi.org/10.18637/jss.v033.i02.
- Janeiro, M. J., Coltman, D. W., Festa-Bianchet, M., Pelletier, F., and Morrissey, M. B. (2017), "Towards robust evolutionary inference with integral projection models," *Journal of Evolutionary Biology*, 30, 270–288. https://doi.org/10.1111/jeb.13000.
- Kruuk, L. E. B. (2004), "Estimating genetic parameters in natural populations using the 'animal model'," *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359, 873–890. https://doi.org/10.1098/rstb.2003.1437.
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., and Coulson, T. (2010), "Coupled dynamics of body mass and population growth in response to environmental change," *Nature*, 466, 482–485. https://doi.org/10.1038/nature09210.
- Partridge, L., and Harvey, P. H. (1988), "The Ecological Context of Life History Evolution," *Science*, 241, 1449–1455. https://doi.org/10.1126/science.241.4872.1449.
- Sheridan, J. A., and Bickford, D. (2011), "Shrinking body size as an ecological response to climate change," *Nature Climate Change*, 1, 401–406. https://doi.org/10.1038/nclimate1259.
- Teplitsky, C., Robinson, M. R., and Merilä, J. (2014), "Evolutionary potential and constraints in wild populations," in *Quantitative Genetics in the Wild*, eds. A. Charmantier, D. Garant, and L. E. B. Kruuk, Oxford University PressOxford, pp. 190–208. https://doi.org/10.1093/acprof:oso/9780199674237.003.0012.
- Yom-Tov, Y., Yom-Tov, S., and Jarrell, G. (2008), "Recent increase in body size of the American marten Martes americana in Alaska: GLOBAL WARMING AND BODY SIZE OF THE AMERICAN MARTEN," *Biological Journal of the Linnean Society*, 93, 701–707. https://doi.org/10.1111/j.1095-8312.2007.00950.x.