

Coping with climate change.

Implications of the Yellow-Bellied Marmot's (*Marmota flaviventris*) body mass evolution in the last half-century.



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Comprehensive exam proposal

by

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Introduction

Climate change (C.C.)

The importance of C.C. and its impact in the near future is no longer in doubt, *at the point where it's sad to have to remind people of them once again.* (Intergovernmental Panel On Climate Change (Ipcc) 2023)

- Broadly, C.C. is [...] (Polar melting, etc.)
- Which even impact human society (e.g., winter in Ottawa isn't the same anymore: Rideau Canal ice skating future is in jeopardy, the number of days with under -20°C is expected to severely decrease in the near future, etc. (!!! + FACT CHECK everything!))
- Main/Precise impacts of C.C. in natural environments
 - **Raising T°:** Explain + study case (!!!)
 - **Changing season length:** Explain + study case (try to find something at RMBL !!!)
 - **Environmental predictability:** Explain + study case (!!!)
 - **Drought events:** Explain + study case (!!!)
 - **Extreme weather events:** Explain + study case (!!!)
 - etc.

Ok, so, now, how does C.C. and these precise perturbations impacts concretely natural population? *Study cases (!!!)*

Body mass as a Life-History Traits (LHT)

Life history traits (LHT) are defined as phenotypic traits (i.e., individuals' characteristics) impacting directly the survival and reproduction (so the fitness) of an individual (Roff 1992).

[...]

For many species, body mass will indeed impact directly these two parameters

Energetic reserves => Impact individuals capacity; Honnest signal of good performance and ressources for sexual competition.

Not only an individual with a high body mass will have more energetic ressources, allowing it to be more resilient to environmental pressure (as this reserves can buffer a low ressource phase for example), but it can also indicate a better ability from the individual to gather ressources, showing better adaptation and survival skills in a given environment. The first consequence of that being an increase of the individual survival with its body mass. But also an individual with more energy will have better capacity to reproduce, and should be more appealing to potential mates in the case of sexual competition, therefore also increasing its reproduction success. Therefore, in many species, body mass can be indeed consider as a LHT.

Link with hibernation

The importance of body mass as a LHT is particularly true for a specific group of species: **Hibernating species**. Indeed, to survive unfavorable season (usually winter in our latitudes) some species disperse to milder environment and other cope with it and find ways to survive through. One adaptation to that is hibernation, which correspond to a state of torpor, individual keeping their metabolism at a survival minimum, surviving on their energetic resources through the winter, emerging at the start of the favourable season. A prerequired adaptation for that kind of behaviour is therefore a large body mass, in order to have enough energetic reserve to stay without resources for a full season. Even more, hibernating species are usually active only for a small part of the year, during which they must gather enough resources, gain enough mass, to survive through next hibernation. So not only a prerequired adaptation is a big body mass, but also the capacity to gain quickly and efficiently body mass in a short amount of time, which represent a lot of challenges and therefore adaptation for the metabolism.

Furthermore, for some species, reproduction occurs right after the hibernation period, which means that before entering into hibernation, individuals must reach a high enough body mass not only to survive, but also to have enough energy left to reproduce right at the start of the active season. Hence, in that disposition, body mass is a keystone LHT for hibernating species biodemography.

In addition to that, we know that climate change is expected to have significant impact on LHT. An impact on body size has even been proposed to be a third universal response to climate change, alongside modification in phenology and geographic range [Gardner et al. (2011); !!! *look for an article explaining the principles of the universal responses to global warming*]

Expected effect of global warming on body mass

As reminded earlier, one of the most significant consequences of climate change is an increase in global temperature (which is why climate change is also commonly referred to as *global warming*, although this term is often used as a rhetoric by climate sceptics during cold winters and violent blizzards¹). This average temperature increase is suspected to influence phenotypic traits such as body mass or size. However, the direction of the response remains uncertain. Some authors argue that a shrinking body size could be one the universal C.C. response (Daufresne et al. 2009). This hypothesis follows Bergmann's rules, which state that smaller body size should be expected in warmer environment as it raises the surface to volume ratio, thus favoring heat dissipation (Bergmann, C 1847). However, as noted by Gardner et al. (2011), a lack of large-scale comparative studies prevent us to demonstrate that this response could be universal. And indeed, several studies at higher latitude yield opposite results (i.e., increasing body mass, Guillemain et al. 2010; Ozgul et al. 2010; Sheridan and Bickford 2011; Yom-Tov et al. 2008). At higher latitudes and altitude, climate change is synonym to milder conditions. As a consequence, individuals have access to a large food supply for a longer time and face less hard conditions during the less favorable season which overall is less energetically demanding, allowing individuals to become larger.

¹“[...] Large parts of the Country are suffering from tremendous amounts of snow and near record setting cold. [...] Wouldn't be bad to have a little of that good old fashioned Global Warming right now!” Donald J. Trump, Jan 20, 2019.

Q.G. and animal models

Body mass and LHT shifts expected with climate change, **evolution** expected.

{To properly estimate the evolutionary signals of a phenotypic change, quantitative genetic gives us a method to decompose the total phenotypic variance (V_P) into its genetic (V_A) and environmental (V_{PE}) part: $V_P = V_A + V_{PE}$.} Quantitative Genetics provides a well-established method for estimating the genetic component of an observed phenotype variation: the **Animal Models** (Kruuk 2004). This method allows a robust estimation of the genetic variance in a trait affected by a large number of genes with small effects (i.e., a “quantitative trait,” Kruuk et al. 2014) by fitting a mixed model with individual identity as a non-independant random effect, linked to a relatedness matrix between each individual, extracted from the population pedigree (i.e., parental link between the individual of a population, !!!). This method has the advantage of being relatively simple to employ, allowing genetic parameter estimation directly from phenotypic data. Only parental links between individuals need to be known, making this method applicable to wild populations (Kruuk 2004; Lynch and Walsh 1996). As emphasized by Kruuk et al. (2014), there is a pressing need for quantitative genetics studies on long-term wildlife populations as the most common problem in that kind of study is the lack of power, which could be adress with long-term studies. Such studies would improve our understanding of the relationship between animals and their environment and of the genotype-phenotype-environment relationship, especially in the context of global change.

LHT coevolution

Traits can’t evolve alone Gould & Lewontin (1979)

Need to show that with multivariate animal model, but no one has enough power for the models (Teplitsky et al. 2014)

POLS

(Dammhahn et al. 2018)

Phenotypic plasticity vs microevolution

Phenotype are expected to be the best fit for specific environment as a result of a long evolution by natural selection (i.e., individuals best adapted to their enviromnent will have better survival and reproductive success, Darwin 1859). However, when this environment changes, as expected in today’s context of climate change, individuals have two solution to avoid disappearance: **disperse** to a more favorable environment, or **adapt** to their new conditions via phenotypic change (Gienapp and Brommer 2014). For adaptation, two further possibilities exist: **phenotypic plasticity**, defined as a change in phenotype expressed by a given genotype (!!! *probably Nussey, I think there’s a book from the late 90’ or early 00’*), which allows for a rapide response within an individual lifetime, is highly flexible and does not involve any changes at the genetic level; and **microevolution**, defined as a change in alleles frequencies in a population over time (!!! *needed?*). {When an individual with a better-fitted phenotype for its new environment appears, it would have a better survival and more reproductive success. If this advantage relies on a heritable genetic difference (i.e., transmitted to its descendants, !!! *needed? something like Lynch & Walsh, for a definition of heritability sensu*

stricto) the new genotype is going to rapidly increase in proportion in the population, ultimately replacing the old one} . Thus, this mechanism can be slow but is a long-term solution when the ecological change is persistent. However if the change is transient, plasticity is a useful mechanism. As noted by DeWitt et al. (1998) and Gardner et al. (2011), phenotypic plasticity solely is unlikely to be the most optimal long-term response to climate change as it is usually a transient answer, presenting costs and limits (DeWitt et al. 1998), to a transient change. Furthermore, if the optimal response to the new environment is a canalized phenotype (i.e., very low phenotypic variance), plasticity can even be maladaptive (Nussey et al. 2007). The expected optimal answer to a long-term environmental change, as caused by climate change, is evolution through natural selection.

Phenotypic plasticity and microevolution are thus not expected to be mutually exclusive. This is particularly evident in highly plastic traits such as body mass which can vary significantly up and down throughout an individual's life in response to among- and within-year changes in environmental conditions but can also change via microevolution at the population level over the same time period .

Nevertheless, as the consequences of these mechanisms can be highly different on the long term (evolution being more permanent than plasticity), quantifying the extent to which each of these mechanisms contributes to the observed change over a long study period remains a challenging but fundamental task to understand the adaptation and evolution of species. This is even more true today, as populations face the numerous challenges brought by global climate change.

So Evolution and plasticity are not mutually exclusive, and even more, evolution can even have an effect on plasticity itself. *Transition with $I * E$ with the reaction norm framework (Nussey et al. 2007).*

$I * E, G * E$ (individual variation in their plasticity)

Plasticity is usually studied using **Reaction Norm framework** (!!! look at DeWitt & Scheiner, 2004; Schlichting & Pigliucci, 1998; West-Eberhard, 2003 from Thibaut's proposal intro), so by studying the value of a phenotypic trait (e.g., body mass, size) in response to an environmental proxy (e.g., temperature, precipitation). A plastic response corresponds to a different phenotypic value associated to a different environment, so by a slope different from 0 for the reaction norm (Nussey et al. 2007). A reaction norm has two parameters: **Elevation** (or "Intercept" in statistical terms), which is the expected phenotypic value in the average environment; and the **Slope** (so "Slope" in statistical terms) corresponding to the linear regression of the phenotype over the environmental gradient, so to estimate the phenotypic response to the environment (i.e., phenotypic plasticity) . So that's how phenotypic plasticity is usually studied. But, as emphasized by Nussey et al. (2007), a lot of information is lost if we just study that at the population level (i.e., by just doing a fixed linear model of the phenotype over the environment). First using a linear mixed model is crucial to estimate different elevations for each individual as commonly there's multiple observation per individual, thus not taking that into account is a violation of the independence application condition (cf every basic stat book) . So doing that allows us to estimate individual variance in the phenotype in the average environment and take into account the fact that all individuals in the population don't have the same base phenotype. However, that kind of model doesn't allow to estimate individual-level difference in their plastic response to the environment, which can be really important biologically and so must be accounted for. Nussey et al. (2007) proposed a framework to estimate that, which is now fairly accepted and used: **Random Regression**. Let's go back to the Linear Mixed Models (LMMs), the "classic" way is to add a random individual term on

the intercept to estimate the “individual variance” by allowing the model to fit one intercept per individual, however in this compilation, the slope is the same for each individuals; now, if we add a random term also on the slope, not only the model estimate one intercept per individual, but also one slope (so basically, one reaction norm per individual), estimating thus the individual variance in the phenotype expected in the average environment (*elevation*) but also the individual variation in phenotypic variation (*slope*) which is commonly called $I * E$.

Once we’ve estimated this between individual variance in plasticity, we can use quantitative genetic methods (i.e., from Animal models, as explained before, but using Random Regression Animal Model: “RRAM”, Nussey et al. (2007)) to decompose this variance into its genetic and permanent environment part to estimate the genetic variation in plasticity, which is called $G * E$. From that we can estimate the heritable variation in reaction norm’s slope and have an idea of the evolutionary potential of phenotypic plasticity in itself.

So we have a really good method to do all that, however, as underlined by Ramakers et al. (2023), if the environmental proxy used for the reaction norm isn’t good enough, a lot of this $I * E$ is missed (what they called a “hidden $I * E$ ”). Furthermore, it’s often impossible to identify the real driver of plasticity in natural conditions (Which is expected as natural environments are exceptionally complex systems, and individuals generally doesn’t have only one environmental variable to deal with...), the real driver can be unknown, unmeasurable are a combination of a lot of different variables (Ramakers et al. 2023). In response to that, the authors proposed a new method, using the Environment Specific Mean phenotype (ESM). Although they’ve shown this method is indeed efficient, they emphasized that we still need a really good knowledge of the studied system, and really specific conditions to be more efficient than the “regular” method. Hence, although it’s a progress, more work is needed to deal with this $I * E$ detection in natural environment problem.

The good news is that we have a really promising, fairly new statistical method that could be applied to that: the “Double Hierarchical Generalized Linear Model” (DHGLM, !!! *find citation + maybe explain a little the method*) [...] from this method we can estimate the *variance in the residual variance* (i.e., “ V_{V_e} ” by estimating the residual variance attributable to each individual). Knowing what these models does (*When I’ll write it*), we’re confident that it can be applied to develop a more powerful method to detect individual variation in plasticity ($I * E$) in natural systems. Indeed, a V_{V_e} significantly greater than 0 should indicate that there is some $I * E$ in the system and would justify investigation by testing different environmental proxies. In contrast, except in very specific conditions, almost impossible in natural conditions (i.e., **perfect** contrary effect), a V_{V_e} equal to 0 indicate that there’s no individual variation in plasticity in the studied system. From this method we should be a way to free ourselves from the problems of bad proxies. And obviously, as for the random regression with the RRAM, we can adapt this method we quantitative genetics to also detect $G * E$ if $I * E$ is detected.

This new method is thus very promising, however, as most new statistical methods, it often poorly understood/used. Hence, a general framework (supervised by someone with good statistical knowledge, i.e., Julien) including the application on how DHGLM could (should) be used to detect $I * E$ would be really helpful for the community (especially with the rising need to study efficiently phenotypic plasticity and its evolution, in natural condition with climate change).

Link with body mass, individual can vary in their growing speed \Leftrightarrow Reaction norm/Plasticity change over time \Rightarrow Evolution directly on the plasticity \Leftrightarrow individual answer to the condition change would be increase their response (i.e., body mass increase within the active season). It would make sense with bet-hedging framework for example

Bet-hedging

(!!! *Ref about bet-hedging*)

Bet on the best fitness for the long term (even if it can mean lower a bit your immediate fitness) to cope with an unpredictable environment. With climate change, environment are less predictable than ever (maybe even more in alpine habitat? !!! *fact check + ref about envmt predictability + focus on alpine habitats*). Thus bet-hedging, for example increase you body size to “buffer” is not a crazy strategy, but can be risky in the future => potential phenological mismatch (i.e., !!! *def + ref about what phenological mismatch is*), bet-hedging is a bet, so you’re not sure to win in the end, and it can end in maladaptation...

Species and study site

A wild Yellow-Bellied Marmot (*Marmota flaviventris*, “YBM”) population in the Upper East River Valley, Colorado, USA, is the subject of one of the longest-term study in the world (1962 - today). YBM is a ground-dwelling sciurid (rodentia, sciuridae) inhabiting alpine habitats in western North America with a life cycle divided between an “active season” representing approximately a third of the year (from May to September) where individuals must forage to reach a threshold body mass in order to survive hibernation for the remainder of the time (Armitage 2014). Individuals experience high seasonal fluctuation in body mass, with a critical threshold to be reached before the onset of hibernation in order to 1) survive through the next active season and 2) have sufficient energy left for hibernation (which occurs in the first weeks of the active season, Armitage 1965, 2014). Consequently, body mass is considered being a critical LHT for the marmots. YBM lives in colonies composed usually by one or more matriline with one adult male, multiple adult females and their offspring (Armitage 2014). Our population is composed of seven main colonies divided between an “up” and a “down valley” with an elevation difference around 300m (“up” = 3,000m; “down” = 2,700m) implying some difference in weather (Armitage 2014; e.g., delayed snowmelt and vegetation growth onset, temperature difference up to 2 °C, Blumstein et al. 2004) and so delayed emergence up to two weeks in the up-valley (Blumstein 2009; Monclús et al. 2014). This two different conditions offers an amazing opportunity to test the impact of environment on several factors while working in natural conditions.

This hibernation (life) cycle is highly environmentally dependant, with the onset and end of the active season believed to be mediated mostly by weather variables such as temperature and snow cover of the region (Armitage 2014). Thus, body mass is expected to be a keystone phenotypic trait for the marmots. It is therefore crucial to understand how this trait and this species responds to global warming, both for conservation purposes and to elucidate links between phenotype and environment.

Body mass increase in YBM

An important body mass increase has been observed in this population over the past half-century (estimated around 600 g for the adult females). Previous studies attributed this major change mostly to phenotypic plasticity (Ozgul et al. 2010). This hypothesis made in fact a lot of sense, with climate change active season is getting longer (milder conditions, higher temperature, less snow, shorter winter, etc.), hence marmots have more time to forage, gain weight, and the hibernation

period is getting shorter so less time for the individuals to lose mass, at the end of the day, we have heavier individuals, makes sense! However, using animal models to properly assess the genetic attributable part of this change, estimating explicitly the body mass' evolutionary signal for the adult females over the time cohort (i.e., year of birth) during the study period, we found an increase, at the genetic scale, estimated around 400 g, with a heritability of 56% (Biro & Martin, Manuscript in progress). So, in fact, around two third of the body mass increase seems to be due to evolution, not just plasticity. Furthermore, although the lengthening active season is indeed a good potential explanation for the body mass increase through phenotypic plasticity, it doesn't match with the observed evolutionary signal. If the main selective pressure on body mass is survival through hibernation (i.e., heavier individuals having more chance to survive through winter as they have more resources), then the expected evolutionary response (i.e., average body mass increase) is occurring when the pressure is decreasing, which doesn't makes sense!

Research objectives & Methodology

Considering that this major phenotypic shift for the YBM in the last half-century has been miss considered, knowing that there is in fact a strong evolutionary signal, we need to reconsider the evolutionary scenario behind this body mass increase.

I will explore which environmental factors could have triggered this shift, but also the mechanism behind this increase and finally the potential implication for the population's future.

Chapter 1 - Mechanisms

Marmot's Biology: What mechanisms are behind the body mass increase?

As emphasized in the introduction, we know that the body mass has increased in the last half-century, however we still know very few about it. And for starter, we don't know yet what has changed in the marmots in the last decades: do they have a bigger constitution (i.e., are they born bigger, their Intercept in statistical term), or does their growing capacity has increased through time (in statistical term again, this would correspond to their slope)?

I * A and G * A

A: AGE => Reaction norm over individual lifetime rather than Environmental gradient

Growth? Baseline? Both?

Double random (Intercept, Slope)

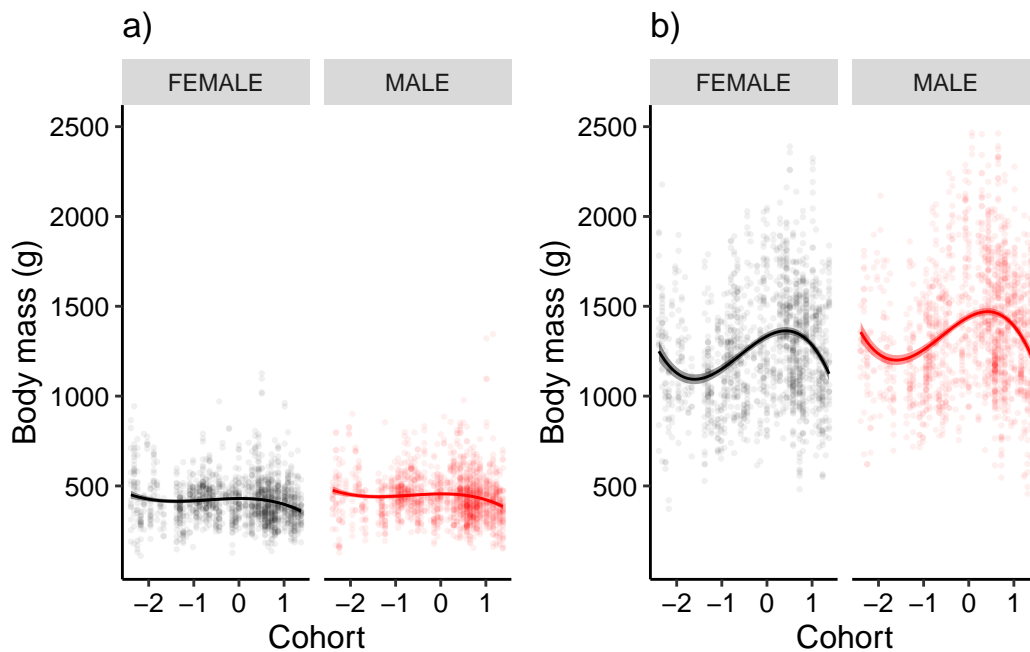


Figure 1: Body mass trend over time cohort for females (black) and males (red) juveniles compared between a) the beginning of the active season (birth weight) and b) the end of the season (mass on August 15th).

Chapter 2 - Methodology

*Methodology: I * E detection with double random mixed models*

(Nussey et al. 2007) → double random

So we're doing something different → examining the residuals of the model (if I * E, still a lot of residual variance ?)

**Look at this one: (Westneat et al. 2015)

DHGLM, brms, Julien's code

Vve (Variance dans la variance résiduel, estime la variance résiduel pour chaque individu et regarde la variance dans cette variance résiduelle, si I * E Vve > 0)

Attention aux modèle débalancés si pas d'effet fixes corrige pour les variations par effet fixes, puis test pour le I * E, si y'en a tu pexu chercher la variable environnemental pour lesquels on a de la variation dans la plasitcité (I * E)

Ned Dochtermann

Chapter 3 - Triggers

Marmot's Biology: Which environmental factors have triggered the phenotypic shift?

E1 - E10 (T°, Precipitation, ...), Seasonal Gradient

Predators, Diet?

Chapter 4 - Implications

Marmot's Biology: What could be the implications of that for the population's future?

Manuscript models Body Mass/active season with survival => Phenological mismatch?? (e.g., thermal stress)

Significance and impacts

References

- Armitage, K. B. (1965), “Vernal behaviour of the yellow-bellied marmot (*Marmota flaviventris*),” *Animal Behaviour*, 13, 59–68. [https://doi.org/10.1016/0003-3472\(65\)90072-2](https://doi.org/10.1016/0003-3472(65)90072-2).
- Armitage, K. B. (2014), *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*, Cambridge University Press. <https://doi.org/10.1017/CBO9781107284272>.
- Bergmann, C (1847), “About the relationships between heat conservation and body size of animals,” *Goett Stud*, 1, 595–708.
- Blumstein, D. T. (2009), “SOCIAL EFFECTS ON EMERGENCE FROM HIBERNATION IN YELLOW-BELLIED MARMOTS.”
- Blumstein, D. T., Im, S., Nicodemus, A., and Zugmeyer, C. (2004), “Yellow-bellied Marmots (*Marmota flaviventris*) Hibernate Socially,” *Journal of Mammalogy*, 85, 25–29. [https://doi.org/10.1644/1545-1542\(2004\)085%3C0025:YMMFHS%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2004)085%3C0025:YMMFHS%3E2.0.CO;2).
- Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., and Réale, D. (2018), “Pace-of-life syndromes: A framework for the adaptive integration of behaviour, physiology and life history,” *Behavioral Ecology and Sociobiology*, 72, 62, s00265-018-2473-y. <https://doi.org/10.1007/s00265-018-2473-y>.
- 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>.
- DeWitt, T. J., Sih, A., and Wilson, D. S. (1998), “Costs and limits of phenotypic plasticity,” *Trends in Ecology & Evolution*, 13, 77–81. [https://doi.org/10.1016/S0169-5347\(97\)01274-3](https://doi.org/10.1016/S0169-5347(97)01274-3).
- 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. (2014), “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>.
- Intergovernmental Panel On Climate Change (Ipcc) (2023), *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press. <https://doi.org/10.1017/9781009325844>.
- 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>.
- Kruuk, L. E. B., Charmantier, A., and Garant, D. (2014), “The study of quantitative genetics in wild populations,” in *Quantitative Genetics in the Wild*, Oxford University PressOxford, pp. 1–15. <https://doi.org/10.1093/acprof:oso/9780199674237.003.0012>.
- Lynch, M., and Walsh, B. (1996), “Genetics and analysis of quantitative traits.”

- Monclús, R., Pang, B., and Blumstein, D. T. (2014), “Yellow-bellied marmots do not compensate for a late start: The role of maternal allocation in shaping life-history trajectories,” *Evolutionary Ecology*, 28, 721–733. <https://doi.org/10.1007/s10682-014-9705-z>.
- Nussey, D. H., Wilson, A. J., and Brommer, J. E. (2007), “The evolutionary ecology of individual phenotypic plasticity in wild populations,” *Journal of Evolutionary Biology*, 20, 831–844. <https://doi.org/10.1111/j.1420-9101.2007.01300.x>.
- 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>.
- Ramakers, J. J. C., Reed, T. E., Harris, M. P., and Gienapp, P. (2023), “Probing variation in reaction norms in wild populations: The importance of reliable environmental proxies,” *Oikos*, 2023, e09592. <https://doi.org/10.1111/oik.09592>.
- Roff, D. A. (1992), “The evolution of life histories : Theory and analysis.”
- 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>.
- Westneat, D. F., Wright, J., and Dingemanse, N. J. (2015), “The biology hidden inside residual within-individual phenotypic variation,” *Biological Reviews*, 90, 729–743. <https://doi.org/10.1111/brv.12131>.
- 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>.