NATIONAL CENTER FOR CASE STUDY TEACHING IN SCIENCE

A Delicate Balance:

Resource Allocation, Immunity, and Disease

by

Emily Cornelius Ruhs, Global and Planetary Health, University of South Florida, Tampa, FL

Cynthia J. Downs, Environmental and Forest Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY

Part I – Why Are Resources Finite?

In the boreal forests of Canada, a small passerine bird, the black-capped chickadee (*Poecile atricapillus*), thrives (Figure 1). Chickadees weigh only about 12 grams and easily fit in the palm of your hand. Despite their small size, chickadees can tolerate mean winter temperatures lower than −25 °C (−13 °F; Petit *et al.*, 2013).

Many bird species migrate to track changes in the availability of a seasonal resource (e.g., food) and avoid freezing temperatures. However, chickadees are part of the larger family, *Parid*, which are resident species, meaning they rarely migrate, and they stay in the same location all year long. Chickadees are widely known for their cognitive abilities, which greatly influence their survival during these freezing temperatures (Sonnenberg *et al.*, 2019).

There are many demanding portions of the annual cycle of a bird (Figure 2, next page) and this is especially true for small birds that must survive during harsh winters. Organisms need to consume a certain number of calories per day to fuel the different aspects of their biological systems, such as brain tissue and blood flow. This amount can be measured by their metabolic rate. For a human, this is about 7530 kJ or 1800 calories per day (Durnin, 1981). For a chickadee, this ranges from 40–65 kJ per day (Karasov *et al.*, 1992; Doherty *et al.*, 2001; Cornelius *et al.*, 2019).

Although chickadees are good at finding food, the acquisition of energy is limited by the amount of food available, predation risk from obtaining that food, and agility for flight (Houston & McNamara, 1993).

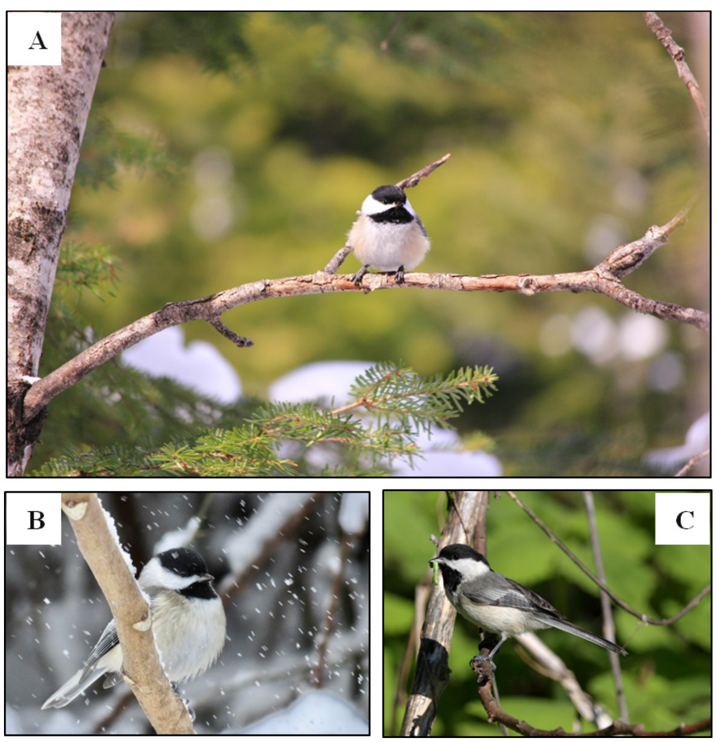


Figure 1. (A) Black-capped chickadee resting on a branch in the boreal forest during winter. Photo by Audrey Le Pogam, used with permission. (B) Chickadee in the snow. Photo by Cam Miller available on FlickR and (C) Chickadee eating a grub. Photo by John Benson available on FlickR. B and C reproduced under a Creative Common license (CC-BY-NC-ND-2.0).

Consider the following before you continue reading: How do both predation risk and starvation risk change with the seasons for a small northern hemisphere bird? When do these two risks intersect in ways that pose especially challenging "decisions" for chickadees?

The amount of food that a chickadee consumes can be thought of as energy that must fuel each of its physiological processes inside the body and outside activities, like flight. These small birds must allocate energy to each of these processes in order to make sure they continue to function properly.

There are a few ways that chickadees gain more energy throughout the day, including foraging to obtain more food or targeting energy-rich foods. Chickadees can also save energy by using something called "hypothermia," meaning they decrease their internal body temperatures to become closer to ambient temperatures and thus reduce heat loss (Chaplin, 1976). However, during hypothermia, birds are generally less responsive and vigilant (Andreasson *et al.*, 2019).

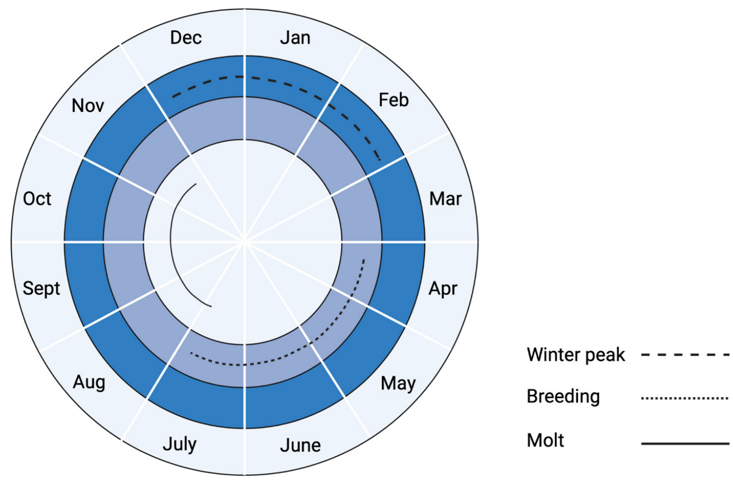


Figure 2. Annual cycle of a black-capped chickadee. The large dotted line represents the peak of winter cold and snow cover. The small dotted line represents the typical breeding season. The solid line represents when molt typically occurs. *Credit:* BioRender academic subscription.

By intaking more food or saving more energy than what is needed on a daily basis, chickadees are able to build up fat stores to help them survive harsh periods.

Questions

1. In a sentence or two, describe the difference between acquisition and allocation.

2. Using Figure 2, list which portions of the annual cycle might be more demanding and why.

3. What information would you need to determine how much energy black-capped chickadees consume on a daily basis?

4. Other than hypothermia, what are some ways that chickadees could conserve energy throughout the day?

5. What might be the short-term consequences of not obtaining enough food (or energy) throughout the day?

Part II – Resource Allocation Across Biological Systems

Adequate fat stores vastly improve nightly and overwintering survival in small birds, including chickadees (Cornelius *et al.*, 2017). In fact, chickadees increase their body mass by 4% (~0.5 g) between the fall and peak of winter (Petit *et al.*, 2013) to cope with the increased energetic needs of living in a cold environment.

Consider the following before you continue reading: Why would chickadees expend more energy when temperatures are cold?

During winter or an extreme weather event when resources are limited (i.e., low food availability), the delicate balance between physiological systems is increasingly threatened. Birds must make a "choice": do they gather more food or trade-off the allocation of energy to the most important processes? Most of the time there is a unconscious trade-off to divert resources to the most important process. During winter, this would mean prioritizing fat storage, because without it, they might not survive the night.

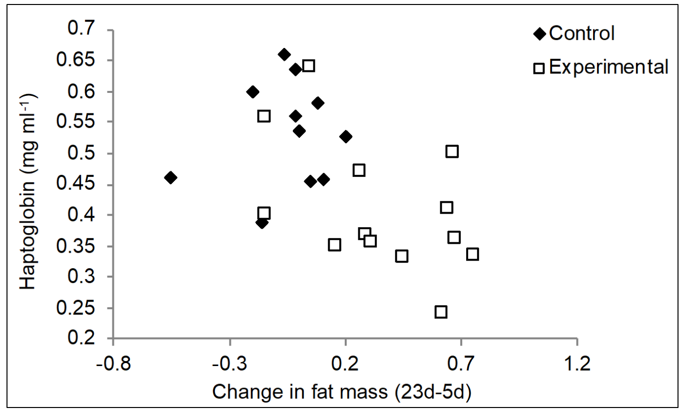


Figure 3. Haptoglobin response, a measure of the inflammatory response versus change in fat mass. Overall, chickadees that had more fat had a lowered haptoglobin response compared to those with less fat reserves. *Credit:* Figure republished with permission of University of Chicago Press–Journals, from Cornelius *et al.* (2017), permission conveyed through Copyright Clearance Center, Inc.

Many have studied the effects of food restriction or unpredictability on the physiology of birds (Bednekoff & Krebs, 1995; Cuthill *et al.*, 2000; Cucco *et al.*, 2002). Chickadees, for example, seem to prioritize short-term survival when faced with food unpredictability in winter-like conditions (−15 °C; see Figure 3). That is, they focus on building up fat stores during cold tempertures ("strategic fattening"; Witter *et al.*, 1995; Houston *et al.*, 2007) over maintaining energetically costly physiological defenses, like the immune response (Cornelius *et al.*, 2017). In fact, it appears that prioritizing fat storage directly traded-off with the ability to mount this immune response (Figure 3).

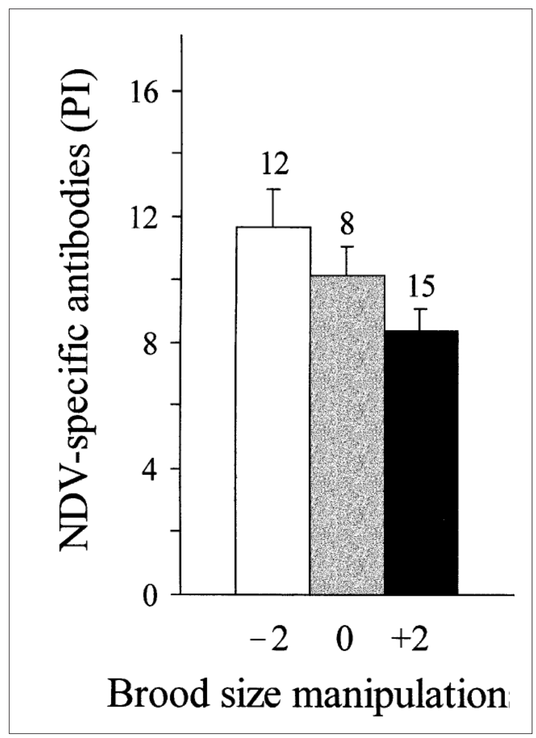


Figure 4. Collared flycatchers with manipulated broods (either increased or decreased by two nestlings). Those with larger broods had decreased antibody production. *Credit:* Figure republished with permission of The Royal Society (U.K.), from Nordling *et al.* (1998), permission conveyed through Copyright Clearance Center, Inc.

As you might have guessed, winter is not the only energetically demanding period; breeding is too. Chickadees have their normal processes they must maintain, but during breeding they must also lay eggs and care for nestlings. Once eggs have hatched, energy demand is at an all-time high as parents must also supply food for their nestlings. This focused attention on providing for themselves and an increased number of nestlings caused adult collared flycatchers (*Ficedula albicollis*) to decrease investment in their antibody production, another type of immune response (Figure 4; Nordling *et al.*, 1998). Similarly, when adult chickadees were given fewer nestlings to care for they had increased body mass compared to those given more nestlings (Cornelius *et al.*, 2019).

However, the summer months are also when parasites and pathogens tend to be most common, as disease carrying insects are more prevalent; this places birds in dangerous situations of needing to prioritize one important function (breeding) over another (defense).

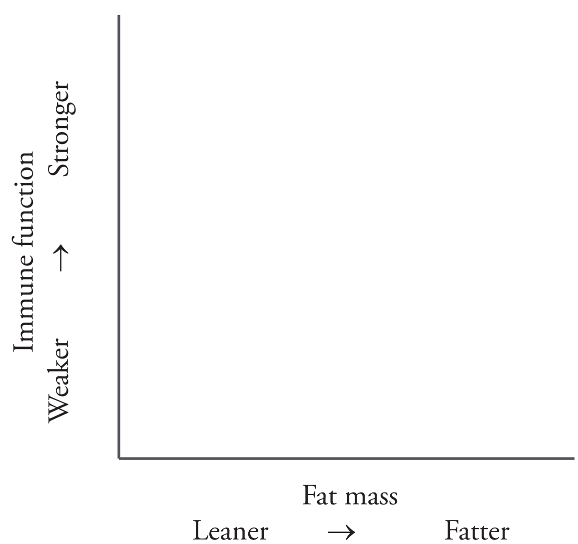
Questions

6. What are the advantages and disadvantages of prioritizing short-term survival (i.e., having adequate fat stores)?

7. How would you design an experiment to test whether animals are experiencing trade-offs between biological systems? What would be some of the things you would measure? What would you need to control?

8. Imagine that you ran an experiment where chickadees were subjected to winter-like temperatures. You designated two groups, a control that got *ad libitum* food (food available at all times) and an experimental group that received reduced food on random days (unpredictable food). At the end of the experiment, you collected the data shown in Figure 3. Describe how you would interpret the graph. What would you conclude?

9. Imagine you have four chickadee populations, during the winter, all with varying amounts of resources available to them.
   Population 1 has more resources than needed to meet its daily energy demands.
   Population 2 has just enough resources to meet its daily energy demands
   Population 3 has not quite resources to meet its daily energy demands
   Population 4 is severely lacking in the resources to meet its daily energy demands
   Draw a point for each population (mean response) based on how you would estimate their relationship between fat mass and immune function. Briefly explain your reasoning.



10. Some bird species are short-lived and invest more into reproduction; others are long-lived and reproduce less often or have smaller clutches. How might trade-offs between physiological systems be impacted by whether a species is short- or long-lived?

Part III – Applying Your Knowledge: Implications for Disease Susceptibility

The ability to mount an immune response is necessary to curb infection with parasites or pathogens. Immune responses vary depending on the pathogen encountered and some responses are more energetically costly to mount than others (Lee, 2006). For example, the inflammatory response, which is similar to the response when you get the flu, can increase total energy expenditure by 16% (Burness *et al.*, 2010). Producing antibodies to a specific pathogen can increase total energy expenditure by 8–25% (Demas *et al.,* 1997; Svensson *et al.*, 1998). This means that certain aspects of immune defense might be more beneficial to downregulate than others (Sheldon & Verhulst, 1996; Lochmiller & Deerenberg, 2000).

Consider the following before you continue reading:
What might a decreased immune response mean for being susceptible to infection (i.e., getting an infection)? Immune defenses are costly; are there certain times of year when it might be important to invest less in aspects of the immune system?

Recall the collared flycatchers from Figure 4. When they had to care for more offspring their antibody production decreased. This led to an overall increase of malarial "haemoproteus" parasites (Figure 5; Nordling *et al.*, 1998). The data from collared flycatchers implies that there is a link between resource availability and disease susceptibility.

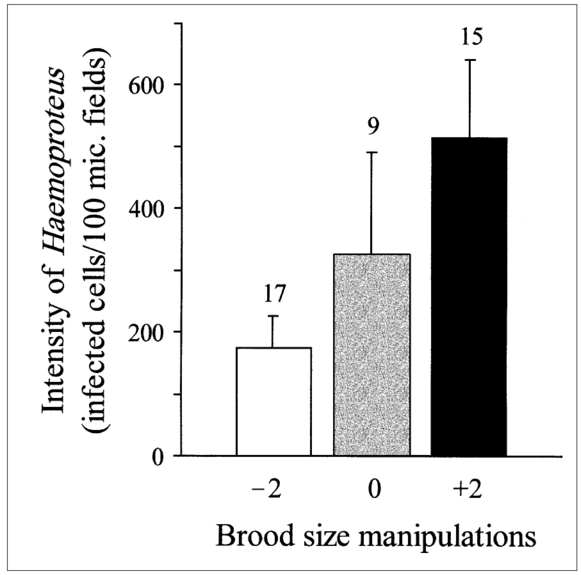


Figure 5. Collared flycatchers with manipulated broods (either increased or decreased by two nestlings). Birds with larger broods had decreased antibody production. *Credit:* Figure republished with permission of The Royal Society (U.K.), from Nordling *et al.* (1998), permission conveyed through Copyright Clearance Center, Inc.

Population density has also been implicated in disease susceptibility. As population density increases the demand and competition for resources also increases, reducing the energetic resources available per individual (Martínez-Padilla *et al.,* 2019) and impacting immunocompetence (the ability to mount an adequate immune response; Lochmiller, 1996).

One interesting example of the relationship between population density and infection is the case of the red grouse (*Lagopus lagopus scoticus*, Figure 6). Red grouse are a gallinaceous bird (ground feeding) that inhabit and feed upon the heathered moors of northern Britain. For many years, researchers have studied their population density and investigated why grouse populations periodically crash (Figure 7, next page). It turns out that, while feeding, grouse ingest a gut parasitic nematode worm, *Trichostrongylus tenuis*. In fact, infection with these parasites strongly influences survival and is implicated, in part, to causing these cyclical population declines (Hudson *et al.*, 1998). Below we'll explore this pattern further in relationship to the concepts we've learned.

Figure 6. Red grouse. *Credit:* Photo by Mark Hope, CC-BY-NC-ND-2, Flickr.

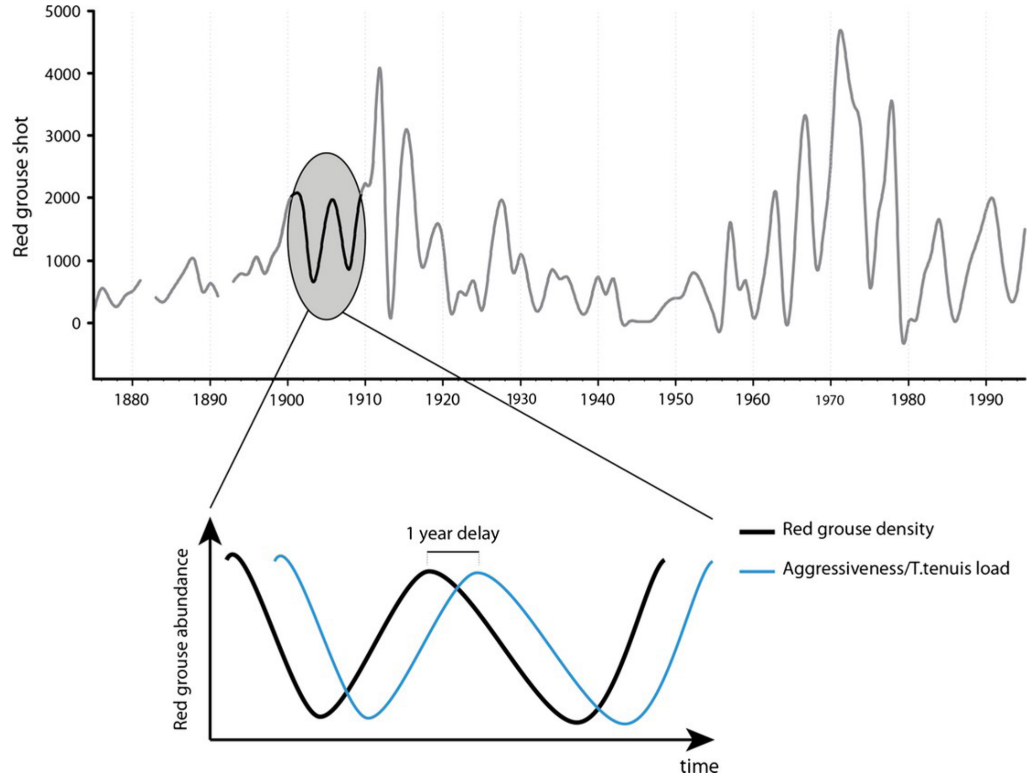


Figure 7. Red grouse population density and parasite load over time. *Credit:* Figure reproduced from Martínez-Padilla *et al.* 2013, courtesy of Wiley-Blackwell Publishing Ltd., used in accordance with publisher's guidelines.

Questions

11. Now that you've gotten to this last section, you're probably thinking, "Wow, this is all so complicated!" You're not wrong. In fact, trade-offs are difficult to study and observe in wild animals, but we can make some educated predictions. Under what conditions would you expect animals to favor survival? To favor maintaining a strong immune response? To favor reproduction?

12. What might a high population density of red grouse mean for the number of parasites present in the moorlands?

13. Mounting an immune response to infection is necessary to fight off infection. In the case of the red grouse, this means fighting off parasitic worm infection. What might be a physiological consequence of mounting a strong immune response? (*Hint:* interpret Figure 8.)

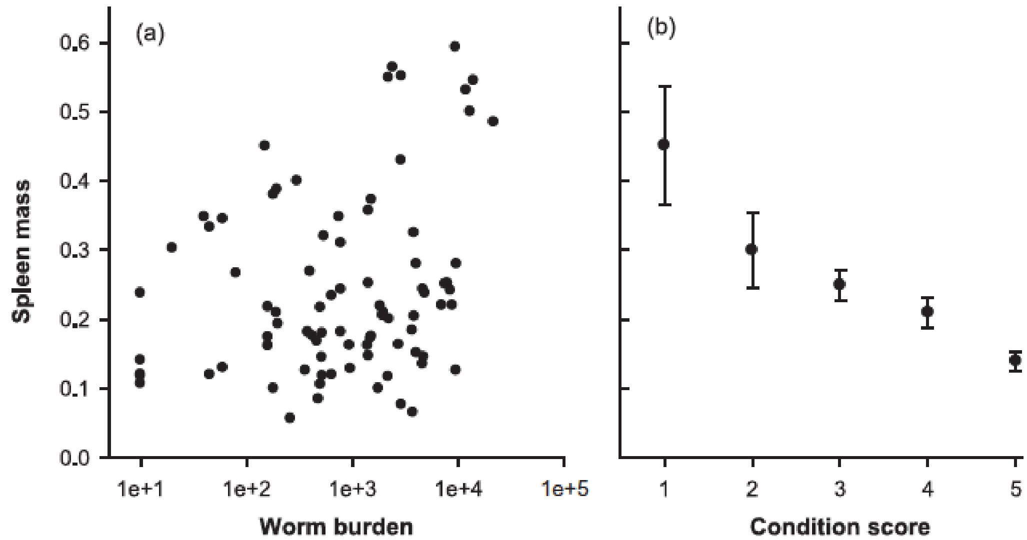


Figure 8. Relationship between spleen mass and worm parasite burden (left) and relationship between spleen mass (proxy for immune response) and body condition score (right); higher score is better. *Credit:* Figure reproduced from Mougeot and Redpath (2004), licensed from John Wiley and Sons.

14. Now you know that resources, immune response and disease susceptibility are all connected. Imagine you are a researcher working on the red grouse system, and you are interested in what would happen if food resources declined (e.g., because of a bad winter, high density of birds). What would you expect to observe, for the grouse population, in terms of:
    a. body mass,
    b. immune response,
    c. parasite infection rates, and
    d. survival.

References

Andreasson, F., A. Nord, and J. Nilsson. (2019). Age-dependent effects of predation risk on night-time hypothermia in two wintering passerine species. *Oecologia* 189: 329–337. <https://doi.org/10.1007/s00442-018-04331-7>

Bednekoff, P.A., and J.R. Krebs. (1995). Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology* 9(3): 457-462. <https://doi.org/10.2307/2390009>

Burness, G., Armstrong, C., Fee, T. & Tilman-Schindel, E. (2010) Is there an energetic-based trade-off between thermoregulation and the acute phase response in zebra finches? *The Journal of Experimental Biology* 213(Pt 8): 1386–94. <https://doi.org/10.1242/jeb.027011>

Chaplin, S.B. (1976) The physiology of hypothermia in the black-capped chickadee, *Parus atricapillus*. *Journal of Comparative Physiology B* 112: 335–44. <https://doi.org/10.1007/BF00692303>

Cornelius, E.A., F. Vézina, L. Regimbald, M. Petit, O.P. Love, and W.H. Karasov. (2017). Chickadees faced with unpredictable food increase fat reserves but certain components of their immune function decline. *Physiological and Biological Zoology* 90(2): 190–200. <https://doi.org/10.1086/689913>

Cornelius Ruhs, E., F. Vézina, M.A. Walker, and W.H. Karasov. (2019). Who pays the bill? The effects of altered brood size on parental and nestling physiology. *Journal of Ornithology* 161(1): 275–88. <https://doi.org/10.1007/s10336-019-01715-1>

Cucco, M., R. Ottonellis, M. Raviola, and G. Malacarne. (2002). Variations of body mass and immune function in response to food unpredictability in magpies. *Acta Oecologica* 23(4): 271–6. <https://doi.org/10.1016/S1146-609X(02)01154-2>

Cuthill, I.C., S.A. Maddocks, C.V. Weall, and E.K.M. Jones. (2000). Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behavioral Ecology* 11(2): 189–95. <https://doi.org/10.1093/beheco/11.2.189>

Demas, G.E., V. Chefer, M.I. Talan, and R.J. Nelson. (1997). Metabolic costs of mounting an antigen-stimulated immune response in adult and aged C57BL/6J mice. *The American Journal of Physiology* 273(5): R1631–7. <https://doi.org/10.1152/ajpregu.1997.273.5.R1631>

Doherty Jr., P.F., J.B. Williams, and T.C. Grubb Jr. (2001). Field metabolism and water flux of Carolina chickadees during breeding and nonbreeding seasons: a test of the "peak-demand" and "reallocation" hypotheses. *The Condor* 103(2): 370–5. <http://www.jstor.org/stable/1370384>

Durnin, J.V.G.A. (1981). Basal metabolic rate in man. Joint FAO/WHO/UNU Expert Consultation on Energy and Protein Requirements, Rome. <http://www.fao.org/3/m2845e/m2845e00.htm>

Houston, A.I., and J.M. McNamara. (1993). A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* 24(3): 205–19. <https://doi.org/10.2307/3676736>

Houston, A.I., J.M. MacNamara, Z. Barta, and K.C. Klasing. (2007). The effect of energy reserves and food availability on optimal immune defence. *Proceedings of the Royal Society B* 274(1627): 2835–42. <https://doi.org/10.1098/rspb.2007.0934>

Hudson, P.J., A.P. Dobson, and D. Newborn. (1998). Prevention of population cycles by parasite removal. *Science* 282(5397): 2256–8. <https://doi.org/10.1126/science.282.5397.2256>

Karasov, W.H., M.C. Brittingham, and S.A. Temple. (1992). Daily energy and expenditure by black-capped chickadees (*Parus atricapillus*) in winter. *The Auk* 109(2): 393–5. <https://doi.org/10.2307/4088213>

Lee, K.A. (2006). Linking immune defenses and life history at the levels of the individual and the species. *Integrative and Comparative Biology* 46(6): 1000–15. <https://doi.org/10.1093/icb/icl049>

Lochmiller, R.L. (1996). Immunocompetence and animal population regulation. *Oikos* 76(3): 594–602. <https://doi.org/10.2307/3546356>

Martínez-Padilla, J., S.M. Redpath, M. Zeineddine, and F. Mougeot. (2013). Insights into population ecology from long-term studies of red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology*, 83(1): 85–98. <https://doi.org/10.1111/1365-2656.12098>

Mougeot, F., and S.M. Redpath. (2004). Sexual ornamentation relates to immune function in male red grouse *Lagopus lagopus scoticus*. *Journal of Avian Biology* 35(5): 425-433. <https://doi.org/10.1111/j.0908-8857.2004.03256.x>

Nordling, D., M. Andersson, S. Zohari, and L. Gustafsson. (1998). Reproductive effort reduces specific immune response and parasite resistance. *Proceedings of the Royal Society of London B: Biological Sciences* 26(1403): 1291–8. <https://doi.org/10.1098/rspb.1998.0432>

Petit, M., A. Lewden, and F. Vézina. (2013). Intra-seasonal flexibility in avian metabolic performance highlights the uncoupling of basal metabolic rate and thermogenic capacity. *PLoS One* 8(6): e68292. <https://doi.org/10.1371/journal.pone.0068292>

Saks, L., Karu, U., Ots, I. & Hõrak, P. (2006). Do standard measures of immunocompetence reflect parasite resistance? The case of Greenfinch coccidiosis. *Functional Ecology* 20(1): 75-82. <https://doi.org/10.1111/j.1365-2435.2006.01068.x >

Sonnenberg, B.R., C.L. Branch, A.M. Pitera, E. Bridge, and V.V. Pravosudov. (2019). Natural selection and spatial cognition in wild food-caching mountain chickadees. *Current Biology* 29(4): P670-676. <https://doi.org/10.1016/j.cub.2019.01.006>

Svensson, E., L. Råberg, C. Koch, and D. Hasselquist. (1998). Energetic stress, immunosuppression and the costs of an antibody response. *Functional Ecology* 12(6): 912–9. <https://doi.org/10.1046/j.1365-2435.1998.00271.x>

Witter, M.S., J.P. Swaddle, and I.C. Cuthill. (1995). Periodic food availability and strategic regulation of body mass in the European starling, *Sturnus vulgaris*. *Functional Ecology* 9(4): 568–74. <https://doi.org/10.2307/2390146>