Biologging wildlife behaviour and the seasonality of boreal food webs

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March 2020

A thesis submitted to McGill University in partial fulfilment of the requirements of the degree of
DOCTOR OF PHILOSOPHY

List of Tables

List of Figures

Abstract

The behavioural decision to be active or inactive represents a trade-off between the need to acquire energy and the costs associated with that acquirement. In seasonal environments, the relative costs and gains associated with activity can shift dramatically between winter, when temperatures are cold and resources are scarce, and summer, when temperatures are mild and resources are abundant. Despite the obvious link between activity and seasonality, studies of activity patterns over multi-seasonal time scales are surprisingly sparse, meaning we do not know how activity responds to environmental conditions and, in turn, how activity responses to environmental conditions influence population dynamics and species interactions. In this thesis, I use biologging to quantify how free-ranging animals adjust activity according to seasonal environmental variation, including air temperature and resource availability, and theoretical modelling to explore the ecological implications of these responses, including population dynamics and trophic interactions. I collected continuous behavioural data through direct observations and biologging technologies over four years on three interacting species - the North American red squirrel, snowshoe hare, and Canada lynx - within the highly seasonal northern boreal forest. Using direct observations for biologger calibration, I show that classifying low frequency accelerometer signatures to long duration behavioural states can be achieved with high accuracy allowing for long duration (weeks to months) recordings even in small mammals with high frequency movements. Combining accelerometric and acoustic biologging technologies on snowshoe hares highlights the complementarity of accelerometer quantification of activity states and acoustic determination of finer-scale details like chewing. I show that red squirrel activity is highly seasonal with a 3-fold decrease in activity from autumn to winter and that hares express subtle behavioural responses to moonlight conditions and are characterized by more seasonal constancy in activity patterns than red squirrels. Given the advances achieved recording behaviour over long time periods on free-ranging individuals, I use four years of accelerometer recordings on red squirrels to show that daily activity is highly predictable as an optimization of energetic and reproductive gain. Finally, I show how summer-to-winter differences in activity levels determines the seasonality of biomass production and loss, and thus population rates of increase, decrease, and stability. Through empirically-supported theoretical modelling, this thesis highlights the ecological importance of animal activity in seasonal environments, including its bottom-up regulation by environmental conditions and its contributions to populations dynamics and species interactions.

Résumé

La décision comportementale d’être actif ou inactif représente un compromis entre le besoin d’acquérir de l’énergie et le coût associé à cette acquisition. Dans les environnements saisonniers, les coûts et bénéfices relatifs associés à l’activité peuvent changer radicalement entre l’hiver, quand la température est froide et les ressources sont rares, et l’été, quand la température est douce et les ressources sont abondantes. Malgré le lien évident entre l’activité et la saisonnalité, les études sur les patrons d’activité à une échelle multi-saisonnière sont rares, ce qui signifie que nous en savons peu sur comment l’activité répond aux conditions environnementales et comment cette réponse influence la dynamique des populations et les interactions entre espèces. Dans cette thèse, j’utilise le biologging pour quantifier comment l’activité des animaux en liberté répond à la variation saisonnière de l’environnement, incluant des changements de températures de l’air et de la disponibilité des ressources, et des modèles théoriques pour explorer les implications écologiques de ces réponses, incluant la dynamique des populations et les interactions trophiques. Dans l’environnement très saisonnier de la forêt boréale nordique, j’ai recueilli, en utilisant des observations directes et des technologies de biologging, des données comportementales en continu sur quatre ans et trois espèces en interaction - l'écureuil roux d'Amérique du Nord, le lièvre d'Amérique et le lynx du Canada. En calibrant les biologgers à l’aide des observations directes, je démontre qu’il est possible de classifier, avec une grande précision, des signatures d’accéléromètre à basse fréquence selon des états comportementaux, ce qui permet des enregistrements de longue durée (semaines à mois) même chez les petits mammifères avec des mouvements à haute fréquence. Chez le lièvre d’Amérique, la combinaison de technologies de biologging en accélérométrie et en acoustique met en évidence la complémentarité des mesures accélérométriques des états d'activité et des mesures acoustiques

plus détaillées du comportement, comme la mastication. Je montre que l'activité des écureuils roux est extrêmement saisonnière avec une activité trois fois moindre à l'automne qu'à l'hiver et que les lièvres expriment des réponses comportementales subtiles aux phases de la lune et un patron saisonnier d'activité plus constant que les écureuils roux. Compte tenu des progrès réalisés sur l'enregistrement du comportement d'individus en liberté sur de longues périodes, j'utilise quatre années d'enregistrements par accéléromètre sur des écureuils roux pour montrer que leur activité quotidienne est hautement prévisible selon l'optimisation des gains énergétiques et reproductifs. Enfin, je montre comment les différences d'activité entre l'été et l'hiver déterminent le caractère saisonnier de la production et de la perte de biomasse, et donc des taux d'accroissement, de diminution et de stabilité des populations. À travers une modélisation théorique appuyée empiriquement, cette thèse met en évidence l'importance écologique de l'activité animale dans les environnements saisonniers, y compris sa régulation ascendante par les conditions environnementales et ses contributions à la dynamique des populations et aux interactions entre espèces.

Acknowledgements

It has been a long, but exciting, journey since I was sitting in Murray's office dreaming up this crazy multi-species project, and the road from there to here was only possible due to the help and support of a large community. First and foremost, I must thank Murray Humphries, whose patience, steadfast support and encouragement, and always-calm demeanor have kept me grounded over the years. We have done some exciting science together that could not have been possible without your ideas, thoughts and questioning mind. You have taught me that a lot can be accomplished by sitting and observing animals, that the best science is science that is done thoroughly, to forage my own path, and to think independently. You have made me into the scientist that I am today and set me up to succeed. Thanks for dropping everything in those few moments of crisis, and for all the long, often quiet, meetings where we let our ideas come together. Most importantly thank you for taking the time to teach me how to write well and to accept that writing takes time. Second, thank you to Stan, my co-supervisor. Your rough exterior and un-filtered opinions have kept me on my toes and often inadvertently gave me the motivation needed to complete projects. I am honoured that I have had the opportunity to work with someone with the wealth of knowledge that you have. You have kept Murray and I's crazy ideas grounded while teaching me how to do ecology. Thanks for all the memories in the field including introducing me to the bunnies and making the lynx project happen.

To the community of Haines Junction, and Champagne-Aishihik First Nations, thank you for welcoming me into your community, giving me a second home, and allowing me to do this research in your backyard. In particular to Agnes Macdonald for allowing us access to her land, and to Lance Goodwin and Mike Crawshay, who as good friends, spent hours talking science and life with me. You both taught me so much about the north and I will always cherish the memories of those chats. Thanks to Andy for teaching me how to actually snowmobile, to Dan Drummond for chats about home and introducing me to fur trapping, to Shawn Taylor, Michelle Oakley, Shane Oakley, and Levy Graham for teaching us how to trap lynx and helping out when we needed advice, and to all the other northerners whose lives I have crossed paths with during this PhD. Also thank you to Carlo Catoni and Technosmart for all of the troubleshooting and remote support over the years with getting the accelerometers working on each species.

To our lab coordinator and good friend, Manu. Thanks for being the rationale voice and sounding board that was always just a phone call away. I will always appreciate the hours that you have spent listening (sometimes in complete confusion) to me talk out the mess of ideas that were in my head. I will greatly miss these conversations, and our annual field adventures/friendly competitions. Beyond Manu, the members of the Humphries' lab have been an incredible support network over the years. Thanks to Jeremy (Rat boy), Quinn, Marianne, Sébastian, Xavier, Victoria, Mélanie, Ally, Bertrand, Joel, Laurence (Yohance), Duncan, Allison 2, Mikhaela, and Gwenyth. Working alongside such a diverse group of people and projects has greatly expanded how I see the world, and I am positive has made me a much more well-rounded person and scientist. I will miss our lab meetings where I was often forced to think outside of the small world of ecology. What I learnt from this group will greatly influence where I go from here.

To winter crew (Mike, Yasmine, and Ally), it has been a crazy PhD journey together. I am so glad that we decided early on to be a team and work collaboratively. This thesis simply would not have been possible without all of your support, hard work, and the data that was collected by each of you. One person simply cannot collect data on three species at once and I couldn’t have asked for a better team of PhD students to have to work so closely with. I will always remember the antics of our long winters stuck in a cabin in the Yukon wilderness and our lengthy discussions about ecology. We’ve all come a long way from the days when it took four of us (and hip hopper) to find a dead bunny. I look forward to all our future collaborations and continuing this journey in science together.

Thank you to Sab, Simon, Lisa, Jess, Yohance, Sam, Sean, Claire, Shannon, Hannes, Manu, Kate (who hates emus), Jacob, Kate (who likes fires), Lindsey, Kevin, Rachael, and Heather, who all gave up part of their lives to help Ally and myself out with chasing squirrels and lynx around the Yukon in the winter. Your hard work and commitment to science was greatly appreciated and critical to the success of this project and thesis. This appreciation extends to all the snowshoe hare technicians that helped Mike and Yasmine out with monitoring the buns each year. Thank you also to all of the KRSP technicians that I have had the pleasure of interacting and working with over the years. You all have played a role in the success of completing a PhD and have taught me so much.

Over the course of this PhD experience, I have been lucky to become part of two long-term collaborative projects. First, the Kluane predator-prey project has essentially become my second family and have provided considerable insight into the ideas that I explored here. Thanks to the established researchers Charles Krebs, Alice Kenney, Rudy Boonstra, Dennis Murray, and Tom Jung, and the up and coming researchers Mel, Jacob, Mike, Yas, Ally, Sam, Rachael, Lee, and

Sho. Your commitment to long-term monitoring and love of the mysteries of the snowshoe hare – lynx population cycle has been inspirational. Second, the Kluane Red Squirrel Project has become a pillar of my graduate education. I feel so lucky to have been a part of such a project that forces you to think about topics and science far outside of what I do. I have learned so much both scientifically and personally from all of you. So thank you especially to Andrew, Ben, Jeff, Jess, Erin, Jack, Andrea, Sarah, Dylan, April, Alex who have all spent hours chatting squirrels with me and providing input on what I was attempting to do.

Thanks to those of you (Melissa, Andrea, Jess, Shannon, Hannes, and Laurence) who had the patience to share an apartment with me and spend evenings chatting about life. Thank you to my adventure buddies that gave me all those much needed breaks from the computer to recharge my sanity. To Erin, Mel, and Lisa, the canoe and hiking trips and escapes from society that I did with each of you will always be fond memories of mine and I am always looking forward to the next one. You've taught me the most important life lesson - laughter is always the best medicine. To Shannon and Hannes, thanks for climbing all those mountains with me and always being there when I needed to get out. Our judgement might not have always been perfect but with no injuries, except to my camera, I'd say every trip was successful and has left me with many good stories. I'll always be up for some more bushwhacking or mountain sledding. And to Rat boy, Yohance, Ed, Emily, and Chandra who took me along on a crazy canoe adventure across the Yukon territory. You were the best group of people I could have spent two weeks in the wilderness with. Thanks for the break from writing and the stories that came from paddling the Crooked Beast over 300 km. Finally, thank you to my parents and family that have quietly

supported me from afar and always encouraged me to chase my dreams. I never would have done this without your support.

A special thank you to all those that supported this research financially including NSERC, Weston Foundation, Wildlife Conservation Society, and NFS.

Contribution to Knowledge

Within this thesis, I contribute to our understanding of how the environment shapes an individuals' choice between activity and inactivity and what implications this choice has on a species' engagement with, and the dynamics of, other species with which it interacts. In achieving this objective, I feel that I have made seven key contributions to knowledge. First by examining behaviour over longer time scales than is typical, this thesis highlights the importance of studying organisms in all seasons. There is a strong bias in research towards studying animals in summer and breeding seasons, but winter is a very different beast that is under appreciated. Within this thesis I show that animals have differential behavioural patterns between seasons (Chapters 2, 4, 5), and more importantly that what occurs in one season has carry-over effects to the other seasons (Chapter 5).

Second, studying behaviour on free-ranging individuals has traditionally been difficult requiring high manpower for little data. Recent advances in technology have alleviated this constraint but required recording behaviour in such fine detail and high frequency that devices were limited in their duration, especially on small mammals that are restricted in the weight they can carry. Chapter 2 pushes the boundaries of what the literature states is the minimal recording frequency that can be used with accelerometers for recording behaviour, and shows that low frequency acceleration data can be used on small mammals with high accuracy if the scale of the behavioural states of interest is increased (e.g., from identifying individual steps to identifying travel bouts). This methodological advance will provide a new way forward within the biologging world and allow more applications of this technology for monitoring behaviour over durations relevant to studying ecological interactions.

The only issue with these technologies is a requirement of species-specific calibrations before the data can be used in behavioural studies. My third contribution to knowledge is a completion of this calibration for red squirrels (Chapter 2) and for snowshoe hares (Chapter 3). Both chapters produced a simple decision tree classification that is easily transferrable to other researchers using accelerometers on these species, as long as the same deployment procedure is used. This has allowed several other research projects in addition to the remainder of my thesis to include continuously-measured behaviour in their analysis.

Fourth, there are limitations in what accelerometers are capable of capturing for which other biologging technologies might be better suited. In Chapter 3, I illustrated the applicability of using acoustic recorders for capturing continuous behaviour on a cryptic species where observing free-ranging individuals was nearly impossible. Although not emphasized in the text, in Chapter 5, I use acoustic recorders on lynx to get continuous data on diet composition. In the first comparison of accelerometer and acoustic recorders on terrestrial fauna, I show the pros and cons of using one technology over another and highlight the importance selecting the right tool for the behaviour of interest. Acoustic recorders are rarely used in terrestrial systems for studying behaviour outside of vocalizations, and the work I have done here should be critical to the incorporation of this emerging method in other work.

Fifth, throughout this thesis, I produce the first detailed characterization of how two boreal species change behaviour over time, contributing new knowledge about the level of flexibility to which red squirrels are capable of adjusting behaviour over a year (Chapter 2 and 4), and how snowshoe hares adjust behaviour in response to moonlight conditions (Chapter 3). The later provided evidence that species use compensatory foraging to minimize daily effects of moonlight-induced activity-reduction during the night.

Sixth, behaviour is often considered to be complex, noisy, and unpredictable but is also often observed at the scale of patch use and prey selection. By zooming out and considering daily scale decisions across seasons and years from a bioenergetic framework, I show that behaviour is actually highly predictable (Chapter 4) and likely bottom-up regulated. Within this chapter, I produce a simple decision model based on optimization of energetic and reproductive gain that should be capable of predicting activity throughout the year for any endotherm given knowledge of resource quality and quantity, temperature, mating opportunities, and energetic parameters.

Finally, I have produced the first attempt, to my knowledge, at incorporating activity into predator-consumer-resource dynamical equations (Chapter 5). In doing so theoretically, I generate testable predictions of how seasonal activity of species influences the flow of energy and biomass through a system. By empirically testing these predictions, I propose that bottom-up regulated seasonal flexibility in activity (Chapter 4) is one of the main determining factors of a population’s rate of increase and decrease, and ultimately the amplitude of cyclical dynamics. This theoretical finding contributes substantially to our understanding of population cycles.

Contribution of Authors

The thesis is manuscript-based with each chapter formatted for the journal in which it was published or will be submitted to. All chapters were conceived and written by me and are a result primarily of my research efforts. M.M. Humphries, as my primary supervisor, provided guidance ideas, critiques and editorial assistance at all stages of the thesis. S. Boutin, as my co-supervisor, also provided ideas, guidance, critiques, and comments on drafts of each chapter.

Chapter 2[1] is published in Ecology and Evolution. The idea to use accelerometers for behaviour in this thesis emerged from a series of conversations between M. Laundre-Currier, M.M. Humphries and myself, to which they are owed partial credit. I designed the collars and field methods, collected the data, scored the videos (with assistance from volunteers), completed all analysis and wrote the manuscript. A.K. Menzies collected some of the data, provided input in the field and comments on drafts. A.G. McAdam, and J.E. Lane are principle investigators of the Kluane Red Squirrel Project who provided advice on study design and editorial comments.

Chapter 3[2] is published in Frontiers in Ecology and Evolution. I designed the collars, field methods, and captive study with input from A.K. Menzies, S. Lavergne, M.J.L. Peers, and Y. Majchrzak. Free-ranging hare data was collected jointly by myself, A.K. Menzies, M.J.L. Peers, and Y. Majchrzak. Boudreau M.R., and Seguin J.L. provided observational and accelerometer data of hare sprints from free-ranging individuals. I analysed all data, conceived the idea of investigating moonlight effects and using audio recorders, and wrote the manuscript. R. Boonstra designed and built the captive facilities, and he and D. Murray are principle investigators of the Kluane Predator Prey Project. All authors provided editorial assistance and suggestions on drafts.

Chapter 4[3] is published in Ecology Letters. I designed the project, analyzed all data, developed the model, and wrote the manuscript. Additionally, most accelerometer data was collected by myself, with the exception of one summer (by E.R. Siracusa), and one autumn (by A.K. Menzies). M.M. Humphries provided assistance in creating the model. A.G. McAdam, S. Boutin, J.E. Lane, and B. Dantzer as the principle investigators of the Kluane Red Squirrel Project oversaw the collection of all core squirrel data used in this paper including resource availabilities, and reproductive parameters. All authors provided input on drafts of the manuscript.

Chapter 5[4] is written for submission to Nature and as such does not have the same distinct sections as the other chapters. I completed all modelling, data analysis, and writing for this chapter. The initial idea stemmed from conversations between M.M. Humphries and myself, which I further developed. K.S. McCann and M.M. Humphries guided and provided input in the development of the model. I collected all red squirrel accelerometer data, I assisted in the collection of the hare accelerometer data in collaboration with M.J.L. Peers, Y.N. Majchrzak, and A.K. Menzies, and I lead the deployment and design of the lynx acoustic recorders while the lynx field work was done in collaboration with A.K. Menzies and R. Derbyshire. M.J.L. Peers provided the survival data for snowshoe hares. A.J. Kenny and C.J. Krebs provided long-term population density data from the CEMP monitoring project that they lead. S. Boutin, A.G. McAdam, J.E. Lane and B. Dantzer provided long-term red squirrel survival and density data from the KRSP project they lead. D.L. Murray, S. Boutin, and M.M. Humphries funded and oversaw the lynx project. Only M.M. Humphries has provided editorial assistance on this chapter at time of submission.

[1] Studd, E. K., Landry-Cuerrier, M., Menzies, A. K., Boutin, S., McAdam, A. G., Lane, J. E., and Humphries, M.M. (2019). Behavioral classification of low-frequency acceleration and temperature data from a free-ranging small mammal. Ecology and Evolution, 9, 619–630.

[2] Studd, E. K., Boudreau, M. R., Majchrzak, Y. N., Menzies, A. K., Peers, M. J. L., Seguin, J. L., Lavergne, S. G., Boonstra, R., Murray, D. L., Boutin, S., Humphries, M. M. (2019) Use of Acceleration and Acoustics to Classify Behavior, Generate Time Budgets, and Evaluate Responses to Moonlight in Free-Ranging Snowshoe Hares. Frontiers in Ecology and Evolution, 17, 154.

[3] Studd, E. K., Menzies, A. K., Dantzer, B., Lane, J. E., McAdam, A. G., Boutin, S., and Humphries, M.M. (in press). The bioenergetic predictability of activity variation across seasons and years. Ecology Letters.

[4] Studd, E. K., Peers M.J.L., Menzies A.K., Majchrzak Y.N., Derbyshire R., Murray D.L., Dantzer B., Lane J.E., McAdam A.G., Kenney A.J., Krebs C.J., Boutin S., McCann K.S., and Humphries, M.M. Bioavailability, ecological dynamics, and the paradox of seasonal enrichment.

Chapter 1 – Introduction

Introduction

The boreal forest, covering 11.5% of earth's land mass is the world's largest terrestrial biome and most seasonal forested environment on earth (Gauthier et al., 2015). Existing in locations where temperatures are below 0°C for 6 – 8 months of the year, these forests are characterized by short growing seasons, severe winters, and low species diversity (Brandt et al., 2013). In order to sustain viable populations, animals residing within these forests must be capable of capitalizing on the short periods of production, and surviving long periods of suspended primary production with associated high energetic costs. While some species take extreme measures to avoid the long winters through migration or hibernation, many remain active and resist conditions through various adjustments and adaptations (Scholander et al., 1950; Marchand, 2013). This variety of behavioural approaches to winter creates seasonal variation in local species composition that is predicted to shift food web regulation from bottom-up in summer to top-down in winter (Humphries et al., 2017).This prediction extends beyond that of hibernators and non-hibernators, with the expectation that there is actually a gradient of behavioural strategies to winter with ramifications on species interactions. However, because the traditional tendency is to study behaviour over short time frames (Lima & Zollner, 1996), or in controlled settings, and to study wildlife during the summer (breeding season) when researchers are free of academic constraints (Marchand, 2013) and environments are considered "active" (Campbell et al., 2005), little is known about behavioural responses of "winter-active" species to seasonal environmental change, especially when measured at a scale that is relevant to population dynamics and species interactions. With the current climate emergency and a push to predict how species will be impacted by milder winters and longer summers (IPCC, 2013), it is critical to collect baseline information year-round on of how species respond to environmental variability.

The objective of this thesis is to determine how an individuals' choice between activity and inactivity is shaped by predictable and unpredictable environmental variation occurring over months, seasons, and years, and how this choice impacts a species' population dynamics and its interactions with other species. This begins with the development of methods for studying behaviour in small mammals over ecologically relevant timescales. Chapter 2 combines behavioural observations with animal-borne acceleration and temperature data from North American red squirrels to develop analytical approaches for classifying low frequency biologging into behaviour and has been published in Ecology and Evolution (Studd et al., 2019). Building on this classification, Chapter 3 evaluates the use of accelerometers and acoustic recorders for recording behaviour on the cryptic snowshoe hare and assesses hare behavioural responses to changing moonlight conditions. This chapter has been published in Frontiers in Ecology and Evolution as part of special issue on biologging (Studd et al., 2019). The remaining two chapters use the classifications developed in Chapter 2 and 3 to examine how animals respond behaviourally to their environment and the population and food web implications of those responses. As such, Chapter 4 examines the drivers of seasonal and multiannual fluctuations in red squirrel activity and develops a bioenergetic model to predict activity according to optimization of energetic gain, and is currently in review at Ecology Letters. Given the predictability of activity at long time scales, Chapter 5 integrates an activity parameter into predator-consumer-resource dynamical equations to assess how variation in seasonal flexibility of a species' behaviour influences species interactions, population rates of increase and decrease, and population stability. This empirically-supported theoretical chapter is prepared for submission to Nature.

In the next section, I review the literature surrounding what behaviour is, how we study it, and how it is influenced by environmental change including seasonality, before concluding with a review of the boreal forest vertebrate food web, and in particular the Kluane ecosystem on which this thesis is focused.

Literature Review

Behaviour – its energetic basis and dynamical consequences

The definition of behaviour is a topic of contention (Levitis et al., 2009; Baum, 2013; Lazzeri, 2014), but fundamentally can be described as a choice that is expressed by an organism, that has a purpose, that takes time, and that occurs in a particular place (Baum, 2013). Although by placing the focus at the level of the organism, this definition admittedly ignores behaviour at the level of neurons (Hogan, 2015), muscles (Grier & Burk, 1992; Manning & Dawkins, 1998), or groups (DeLellis et al., 2015), but in doing so does focus in on a level that is relevant to the ecology of a species (Baum, 2013). Even after narrowing the definition to a specific level of organization, the form that behaviour takes is still highly varied, both occurring across many axes of variation (including but not limited to movement, feeding, and social behavior), and across different timescales (from seconds to seasons; Bailey et al., 1996; Mueller & Diamond, 2001; Owen-Smith et al., 2010). For example, depending on the question of interest, one could describe the behaviour of an animal as a set of steps and pauses, a sequence of feeding and sleeping bouts, or a transition between migrating and non-migrating. This wide range of categorizations represents a variety of different contexts and questions that can be explored. Ultimately, both the form and definition of behaviour that is used will depend on which of Tinbergen's four questions (or other more recently proposed behavioural frameworks; see Hogan 2015) the particular study of behavior is directed under (Tinbergen 1963, Batesen and Laland 2013). For the purpose of finding a generalizable way to classify behaviour across all species in a manner that is pertinent to the ecology of the species and its interactions with the environment and other species, the rest of this review will consider behaviour in the form of two contrasting states: activity and inactivity. In this form, activity, defined as moving, feeding, and outside of a refuge, is characterized by acquisition and expenditure, and inactivity, defined as stationary, not feeding, and within a refuge, is characterized by conservation and recuperation.

Behavioral variation is widely recognized as important in defining an animal's energetic status, and as such is highly dependent on environmental conditions. All animals are essentially energy processors that take energy acquired from the environment and allocate it to maintenance, growth, and reproduction (Yodzis & Innes, 1992). In this light, the choice between activity and inactivity defines both energy intake and expenditure; energy intake is determined, in part, by time spent foraging, and energy expenditure is determined by the cost of the behaviour, as well as costs of thermoregulation (Anderson & Jetz, 2005; Humphries & McCann, 2014). With clear links from foraging theory that foraging time is dependent on resource availability, resource quality and predation risk (Pyke, 1984; Houston & Mcnamara, 2014), and from metabolic theory that energy expenditure is dependent on thermal conditions (Scholander et al., 1950; Buckley et al., 2018), whether activity generates an energy surplus or deficit, and thus whether an animal should be active or inactive is ultimately environmentally-driven. Despite the obvious connection between behaviour and environmental conditions, and behaviour and energy status, our consideration of behaviour in energetic processes is often neglected (Kam & Degen, 1997; Humphries & Umbanhowar, 2007). But it is through these two connections, and through consideration of behaviour in these processes that we can begin to understand the relationship between environmental variation and life-history and ecological outcomes.

In addition to its role in energetic pathways, behavioural variation also shapes the nature and strength of ecological interactions (Rizzuto et al., 2018). Food webs are shaped by the outcomes of behavioural decisions oriented around the discordant interests of predators seeking to eat prey, and prey seeking to avoid being eaten by predators. Initial attempts to incorporate behaviour into ecological theory focused on handling time constraints that limit the consumption of abundant prey (i.e. saturating functional responses), and search image constraints that limit the consumption of scarce prey (i.e accelerating functional responses; Holling, 1959, 1966; Rosenzweig & MacArthur, 1963). With the inclusion of prey choice (MacArthur & Pianka, 1966) and habitat selection (Fretwell & Lucas, 1969) into basic ecological theory, behaviour came to be recognized as a choice in addition to a constraint. However, these foundational models and the modern food web theory that is organized around them omit many additional behavioural decisions that must be critical to food web interactions. In particular, the behavioural decisions made by a consumer, seeking to acquire a resource in the presence of a predator are likely to be highly complex and sensitive to resource abundance, predator abundance, predator behaviour, and multiple aspects of the abiotic environment (e.g., photoperiod, temperature, snow and ice cover, etc.; Schoener, 1971; Pyke et al., 1977; Sih, 2005; Laundré et al., 2010; van Beest et al., 2012; Dell et al., 2014). The form of these decisions – how animals behave in time – will determine not only the interaction strength between two species, but also whether a modification in one component of a food web will influence the stability of adjacent components of that food web (i.e. indirect effects, trophic cascades; Pace et al., 1999; Werner & Peacor, 2003; Schmitz et al., 2004). It is thus important, that we begin to explore the role behaviour plays in food web theory by considering it from a bioenergetic framework.

Measuring behavior in the wild

Recent advances in technology are revolutionizing methodological approaches and alleviating long-standing constraints of studying behaviour of free-ranging organisms. Traditionally behavioural research has relied heavily on direct observations of free-ranging species (Altmann, 1974), a process that required large manpower for little data, was restricted to non-cryptic species, and was marred by the fact that individuals would often adjust behaviour in the presence of an observer (Schneirla, 1950; Altmann & Altmann, 2006; Crofoot et al., 2010). The use of indirect methods like tracking, and camera traps gave access to times and species where observation was not possible, but still provided only a brief snapshots of behaviour (Macdonald, 1978; Priede & Swift, 1992; Meek et al., 2014; Caravaggi et al., 2017). These limitations meant quantifications of behaviour could only be achieved at broad classifications and often only at a population level over a whole season. Recently, the biologging revolution, as part of the broader digital revolution and the entrance of the world into the Information Age has brought drastic shifts to how behaviour is studied (Brown et al., 2013; Kays et al., 2015). The constant reduction in the size of computers and microprocessors resulting from a doubling of the number of processors per microchip every two years (i.e., Moore's law) has led to an equivalent improvement of animal attached remote sensors, or bio-loggers (Moore, 1965; Elliott, 2016).

This is producing opportunities for continuous and detailed recordings of behaviour during cryptic times and in cryptic locations over long time periods, thus eliminating the previous limitations imposed by requirements for physical observations or hands-on measurements (Ropert-Coudert & Wilson, 2005; Hussey et al., 2015; Wilmers et al., 2015).

With an explosion of bio-logging technologies and the ever-increasing processor efficiencies, ecologists now face the task of choosing the right tool for the right job. A plethora of bio-loggers exist that are capable of collecting a range of data about individuals and their local environment through measurements of spatial location (Cagnacci et al., 2010; Dujon et al., 2014), proximity (Prange et al., 2006), acceleration (Yoda et al., 1999; Gleiss et al., 2011), temperature (Brown-Brandt et al., 2003; James & Mrosovsky, 2004; Kanda et al., 2009), depth (Hays et al., 2007), heart rate (Woakes et al., 1995; Ropert-Coudert et al., 2009), sound (Lynch et al., 2013; Couchoux et al., 2015), and video (Thompson et al., 2012; Rutz & Troscianko, 2013). Every device provides a wealth of information but three technologies in particular capture detailed information on behaviour without the need of an observer. Camera collars produce videos taken from the perspective of the animal, notably providing information on prey selection, inter- and intra-species interactions, and local environmental conditions (Thompson et al., 2012; Pagano et al., 2018). Although there is lots of potential in the camera collars, as of yet the high energy consumption limits their application to large animals who can carry the weight of the battery. Acoustic recorders first gained attention for documenting soundscapes (Pijanowski et al., 2011), and animal communication (e.g., Reby & McComb, 2003; Fischer et al., 2004; Couchoux et al., 2015; Thiebault et al., 2016) but more recently have also showed great potential in also recording non-vocal behaviour, even on small mammals (e.g., flying, feeding, walking; Ilany et al., 2013;

Lynch et al., 2013; Stowell et al., 2017; Wijers et al., 2018). Accelerometers that record the magnitude and direction of proper acceleration along multiple axes at high frequencies can provide information on the movement, activity, energy expenditure, and behaviour of individuals in fine detail over large temporal scales (e.g., Shepard et al., 2008; Nathan et al., 2012; Bidder et al., 2014; Williams et al., 2014).

With each biologging device comes methodological challenges that can limit their applicability for answering ecological questions. The three technologies mentioned above, that are useful for behavioural studies, require recording at high frequencies in order for the data to be convertible to behaviour (see recommendations in Brown et al., 2013). This necessity results in high energy consumption which on small mammals, in particular, means only short deployments and thus still only snapshots of behaviour through time (Tatler et al., 2018). However, little work has been done to explore the possibility of extracting behaviour from lower frequency data, which if possible could provide a way to extend deployments. The other limitation is that conversion of biologger data into behaviour can require large processing power, partly due to the use of machine learning algorithms like random forests (Breiman, 2001; Nathan et al., 2012; Campbell et al., 2013; Graf et al., 2015). Unfortunately, these methods have a black box nature that makes it difficult for researchers to assess the logic, validity, and accuracy of a classification developed with training data and applied to new applications lacking training data (Bidder et al., 2014; McClune et al., 2014). To counter this, support is gaining ground for more simplified techniques that, although are more time consuming, produce results in a more comprehensible classification that is easily transferrable to new applications (e.g., Collins et al., 2015). Given these limitations, there remains a need for further methodological exploration of the techniques used for biologging behaviour.

Behavioural responses to changing environments

All environments change cyclically over time at various scales and magnitudes that influence how animals choose to behave. At one of the shorter timescales, the rotation of the earth around its axis creates a transition from day to night that brings drastic changes in the light environment and a corresponding daily fluctuation in temperature. This simple transition maintains circadian rhythms and generates daily activity patterns as individuals select the environmental conditions that best suit its needs (Daan, 1981; Anderson & Wiens, 2017; Yan et al., 2018; Vinne et al., 2019). Over the course of each month, the rotation of the moon around the earth creates a lunar cycle which adjusts the level of light available each night for nocturnal animals. With light levels determining visual acuteness, moonlight conditions are known to impact hunting success of visual predators, as well as perceived predation risk for prey (Daly et al., 1992; Pratas-Santiago et al., 2016). At the scale of a year, the rotation of the earth around the sun creates seasons. These long term changes in photoperiod and temperature drive primary productivity, often resulting in an environment that fluctuates annually between scarce resources combined with harsh thermal conditions, and abundant resources combined with thermally neutral temperatures (Goward et al., 1985). The duration of these seasonal fluctuations extend past the length that animals can just sit and wait until conditions return to being favourable, and thus require more drastic behavioural adjustments (Goldman, 2001). Some species avoid harsh seasons by migrating or hibernating, while others remain active and resist conditions by adjusting behaviour where possible (Lovegrove, 2000; Marchand, 2013). Whatever the strategy, these seasonal fluctuations are responsible for creating annual routines that structure the year into discrete periods (i.e., breeding season) (McNamara & Houston, 2008). Regardless of the scale over which environmental conditions vary, cyclic changes in light and temperature are always key predictors of behavioural variation (Laje et al., 2018).

In addition to these predictable changes in the environment, animals also face unpredictable and non-cyclic environmental variability. Short-term variation in weather is often unpredictable and can drastically change the local environment. Wind, rain, snow, drought, and floods affect thermal conditions and resource availability in ways that augment behaviour by shifting energetic costs and gains (Kemp et al., 2010; Ismail et al., 2011; Payne et al., 2013; Loe et al., 2016). Most primary resources grow on an annual cycle in connection with seasonality, but the quantity and quality of plant growth and seed production varies each year with climate, as well as with masting events that have evolved through plant-herbivore arms races (Yang et al., 2010; Sala et al., 2012). These two processes create multiannual fluctuations including intermittent pulse resources on which animals are known to adjust reproduction and activity in response to (Boutin et al., 2006; Yang et al., 2008; Bergeron et al., 2011). Finally, climate change is expected to bring more unpredictable weather and extreme events, in addition to shifting the characteristics of each season, including a shortening of winter, and lengthening of summer as the climate generally warms (Reed, 2006; IPCC, 2013). Responses to shifting seasons and extreme weather are varied and species- and location-dependent, but can include anything from reproductive mismatch and population crashes, to range expansions and increased production (Hellberg et al., 2001; Wilson et al., 2005; Both et al., 2006; Durant et al., 2007; Wong & Candolin, 2015).

Despite knowing that animals respond behaviourally to changing environments, most research thus far has focussed on the short term responses, extreme behaviours, or broad responses, leaving long term variation as far less understood. For example, the characterisation of daily activity patterns is one of the most ubiquitous metrics collected of any animal, but seasonal activity patterns are mainly only quantified in animals with extreme responses like hibernation or migration. With climate change becoming a critical issue that the world is facing, and an ever-growing desire to predict what the effects on wildlife will be, filling the gaps in our understanding of species responses to predictable and unpredictable environmental change will become crucial. Included within this is the need to collect baseline data on, and explore how species that don't exhibit extreme behaviour respond to environmental variation occurring over long time frames like seasons, as these are the processes that are most likely to be affected by climate change.

The northern boreal forest and Kluane

The boreal forest, as the world's coldest forest ecosystem, constitutes a quarter of the planet's closed canopy forests, and is home to some of the most dramatic population cycles. With a circumpolar distribution, this biome is characterized by conifer forest and low biodiversity relative to lower latitudes, but species composition and community structure varies between geographic regions (Brandt et al., 2013; Boonstra et al., 2016). Much of the boreal forest is well known for the presence of large population cycles of small mammalian species, although the primary species that cycles differs between the regions (North America: hares, Krebs et al., 1995; Siberia: shrews, Zakharov et al., 1997; Europe: voles, Sundell et al., 2013). In the northern boreal forest of North America, the dramatic rise and fall in the numbers of snowshoe hares and lynx was first documented in 1830 in Hudson Bay Company written records of fur returns (Poland 1892). For the nearly 200 years since, the ten year lynx-hare cycle has drawn the attention of many of the world's top ecologists including Charles Elton (1942), AWF Banfield (1951), Pat Moran (1953), Robert May (1980), Charles Krebs (1995), and Nils Stenseth (1999). More recently the lynx-hare cycle, and its ramifications on the entire boreal food web, has been intensively studied in south-western Yukon between 1980 and present (Krebs et al., 2018) and is where the work for this thesis was carried out.

The Kluane region of southwestern Yukon (61°N, 138°W) is defined by its relatively high elevation and its location in the climatic rain shadow of the St. Elias Mountains. These unique characteristics manifest in a colder climate and generally lower productivity than areas to the northeast and southwest (Krebs et al., 2001). The study occurred in the Shakwak trench, a 8-12 km wide valley that is bordered by Kluane National Park and the St. Elias Mountains to the west, and the Kluane Ranges to the east. This valley runs south for 50 km from Kluane Lake. Aside from the Alaska Highway that transects the valley, a couple of cabins at the southern edge, the area is essentially uninhabited and with the establishment of the Kluane Game Sanctuary in 1942, the area between the highway and the St. Elias Mountains is protected from overexploitation of wildlife. In addition traditional land claims have been signed for sections of the valley. The climate in the region is highly seasonal, with day length ranging from 22 hours to 5 hours, and monthly mean temperatures fluctuating from 20°C to -35°C between summer and winter. Snow typically starts to accumulate in October and remains until May restricting the growing season to three months (Krebs et al., 2001).

The boreal forest, and in particular the mammalian species that reside within this region, have been the focus of studies and long-term monitoring projects for the past 40 years making them well characterized. The forest is predominantly white spruce (*Picea glauca*) intermixed with patches of aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), and an understory of gray willow (*Salix glauca*) and dwarf birch (*Betula pumila var. glandulifera*) (Boonstra et al., 2016). The herbivore community is dominated, in terms of biomass, by snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*), and to a lesser degree by moose (*Alces alces*) and small rodents while the predator community primarily consists of lynx (*Lynx canadensis*), coyote (*Canis latrans*), and birds of prey (Krebs et al., 2001). The dynamics of most species within the forest are linked to the 10-year population cycles of the snowshoe hares, except for the red squirrel which cycles in response to spruce cone masting events (Krebs et al., 2014). This thesis is focused on a subset of the species in this region, the snowshoe hare, Canada lynx, and red squirrel, and the interactions that occur between them, and that occur with their resources.

Snowshoe hares are considered the keystone species of the boreal forest. Their diet consists of forbs, leaves and terminal twigs of shrubs in summer but during the long winter they subsist only on twigs and bark of shrubs, and spruce needles once the snow is deep enough to prevent digging for forbs and grasses (Wolff, 1978; Smith et al., 1988; Hodges, 2000; Seccombe-Hett & Turkington, 2008). High availability of resources in summer is converted into high production with hares having up to 4 litters of 3-5 leverets per year (Stefan & Krebs, 2001). Mortality is high and primarily due to predation, with most hares not living to reproductive age (Krebs et al., 1995). Hares are primarily active through the night including during crepuscular periods with greater distances travelled per night in winter than summer (Keith, 1964; Mech et al., 1966; Feierabend & Kielland, 2014). As nocturnal animals, hares are known to respond behaviourally to changing moonlight conditions by adjusting habitat selection and in some populations distance travelled (Griffin et al., 2005; Gigliotti & Diefenbach, 2018). However, most of our knowledge of activity and behavioural responses has come from monitoring movement spatially (e.g., displacement) which may not accurately represent the amount of activity within a time period.

Red squirrels are seed-eating rodents whose populations are desynchronized from the hare-lynx cycle by white spruce cone masting episodes that occur every 4-5 years (Boutin et al., 1995, 2006). This arboreal species is a capital breeder reliant on white spruce seed and fungi that is hoarded when available and consumed throughout the winter and into breeding (Archibald et al., 2013; Fletcher et al., 2013). In this northern population, females generally have only one litter of 2-4 pups per year except in years when the white spruce mast (McAdam et al., 2007, 2019). In these years, squirrels anticipate the coming resource availability and continue breeding through the summer and into the autumn producing two litters. As such population dynamics are driven by white spruce seed availability, peaking in autumns following masting events (Krebs et al., 2014). Despite their small size (200g), squirrels remain active above ground throughout the winter building well-insulated grass nests in the trees to reduce energy expenditure when resting (Humphries et al., 2005; Guillemette et al., 2009). Both activity patterns and diet vary seasonally with timing of activity shifting from the warmest to coldest part of the day, and diet shifting from hoarded resources to buds, and fresh mushrooms or cones as winter transitions into summer (Fletcher et al., 2013; Studd et al., 2016). Little consideration has been given to downstream effects of seasonal fluctuations in resources on behaviour or how fluctuations in behaviour may impact higher trophic levels.

Our detailed knowledge of these two herbivores and their predators in Kluane provides an ideal system to achieve the objectives of this thesis. Snowshoe hares and red squirrels are apparent competitors with differing diets and life histories but shared predators including both mammalian (coyote, Canada lynx), and avian (Northern goshawk: *Accipiter gentilis*, great-horned owl: *Bubo virginianus*) species. Snowshoe hares are primarily consumed by Canada lynx and secondarily by coyotes (Peers et al., submitted; Krebs et al., 2001). Red squirrels are primarily consumed by avian predators and secondarily by mammalian predators (Stuart-Smith & Boutin, 1995). Lynx are known to switch from snowshoe hares to red squirrels when hares are at low abundance, while coyotes switch to squirrels and red-backed voles during the same conditions (O'Donoghue et al., 1998). This wealth of knowledge, the existence of several long-term monitoring projects of the small mammal communities and their predators that reside in this area, and the highly seasonal environment make it an ideal study system to explore questions surrounding behaviour and seasonality.

Chapter 2 - Behavioral classification of low frequency acceleration and temperature data from a free ranging small mammal

Abstract

1. The miniaturization and affordability of new technology is driving a biologging revolution in wildlife ecology with use of animal-borne data logging devices. Among many new biologging technologies, accelerometers are emerging as key tools for continuously recording animal behavior. Yet a critical, but under-acknowledged consideration in biologging is the trade-off between sampling rate and sampling duration, created by battery- (or memory-) related sampling constraints. This is especially acute among small animals, causing most researchers to sample at high rates for very limited durations. Here, we show that high accuracy in behavioral classification is achievable when pairing low frequency acceleration recordings with temperature.

2. We conducted 84 hours of direct behavioral observations on 67 free-ranging red squirrels (200-300 g) that were fitted with accelerometers (2 g) recording tri-axial acceleration and temperature at 1 Hz. We then used a random forest algorithm and a manually-created decision tree, with variable sampling window lengths, to associate observed behavior with logger recorded acceleration and temperature. Finally, we assessed the accuracy of these different classifications using an additional 60 hours of behavioral observations, not used in the initial classification.

3. The accuracy of the manually-created decision tree classification using observational data varied from 70.6% to 91.6% depending on the complexity of the tree, with increasing

accuracy as complexity decreased. Short duration behavior like running had lower accuracy than long duration behavior like feeding. The random forest algorithm offered similarly high overall accuracy, but the manual decision tree afforded the flexibility to create a hierarchical tree, and to adjust sampling window length for behavioral states with varying durations.

4. Low frequency biologging of acceleration and temperature allows accurate behavioral classification of small animals over multi-month sampling durations. Nevertheless, low sampling rates impose several important limitations, especially related to assessing the classification accuracy of short duration behavior.

Introduction

In recent years, accelerometers have become an important tool in ecology, initially used in marine ecosystems where direct observations are difficult and the need for a device that records what cannot be observed was necessary (Yoda et al., 1999; Brown et al., 2013). Since then, there has been a slow integration of these dataloggers by terrestrial wildlife biologists to aid in the quantification of energy expenditure, activity levels, and animal behavior (Wilson et al., 2008; Gleiss et al., 2011). An exciting opportunity afforded by biologgers is the potential to document how the behavior of free-ranging animals, including their time budgets (e.g., McClintock et al., 2013), movement rates (e.g., Heurich et al., 2014), and occurrence of specific acts like predation (e.g., Williams et al., 2014), mating (e.g., Whitney et al., 2010), specialized feeding (e.g., Watanabe & Takahashi, 2013), or refuge occupation (e.g., Körtner & Geiser, 2000), corresponds with temporal variation in temperature, photoperiod, and resource availability operating over daily (e.g. photoperiod), monthly (e.g. moon phase), annual (e.g., seasons), and multi-annual time scales. However, constraints related to biologger battery life, memory capacity, and device size generate a trade-off between sampling rate (frequency of recording) and sampling duration (the recording interval between the start and end of observations). While high sampling rates are attractive because they offer more accurate information at higher temporal resolution, they often require sampling durations that are much shorter than many ecologically-important timescales. Small animals that cannot carry large biologgers are most constrained in this way.

The sampling rate vs. duration trade-off is made more extreme with accelerometers by the recommendation that recording frequencies need to be at least twice that of the highest frequency movement of the individual (Brown et al., 2013). For small species, which consequentially have the highest stride frequencies (Bejan et al., 2006), this requires a recording frequency between 8 and 100 Hz (Brown et al., 2013). This results in a potential maximum recording longevity in the order of minutes to days, unless sub-sampling techniques are used (e.g. Hammond et al., 2016). Unfortunately, such short sampling duration severely constrains the forms and extent of temporal variation that can be incorporated into behavioral studies. An alternative method is to extend the sampling duration by reducing the sampling rate. If behavioral classification is possible at recording frequencies of 1 Hz or slower, sampling period could be increased from hours or days to weeks, months, or years, again depending on the size of the tag possible given animal mass. However, the few studies that have directly tested this possibility suggested that low recording frequencies have significantly reduced accuracy when using current classification methods (Broell et al., 2013; Wang et al., 2015; Pagano et al., 2017).

For species-specific calibrations, a variety of methods have been proposed for the conversion of raw acceleration values into behavioral states (Nathan et al., 2012; Bidder et al., 2014; Collins et al., 2015). Many methods use supervised machine learning algorithms and among the most popular methods is the random forest algorithm (Breiman, 2001), which uses known data to generate numerous decision trees and calculates the overall relative importance of each variable with which it was provided (e.g. Graf et al., 2015). The black box nature and data specificity of these methods makes it difficult for researchers to assess the logic, validity, and accuracy of applying classification schemes developed with training data to new applications lacking training data (Bidder et al., 2014; McClune et al., 2014). As alternatives to such methods, arguments have been raised for more simplified analytical techniques such as manually creating decision trees (Collins et al., 2015). Although more time consuming, the hands-on nature of this approach, likely results in a more comprehensible classification that should be more easily transferable to new applications.

In addition to acceleration, many accelerometer devices designed for wildlife research are equipped with built-in temperature loggers (e.g. Figure 2.1). Although often overlooked and under used, recorded temperature can provide important supplementary information about an individual and its thermal micro-environment. When attached externally to an animal, the temperature recorded is often intermediate between body temperature and the ambient temperature of the environment immediately surrounding the individual (Osgodd & Weigl, 1972; Tremblay et al., 2003; Studd et al., 2016). This temperature intermediacy likely accounts for their rarity of use; collar temperature is not a reliable measure of body temperature or air temperature (Audet & Thomas, 1996; van Beest et al., 2012). However, depending on the

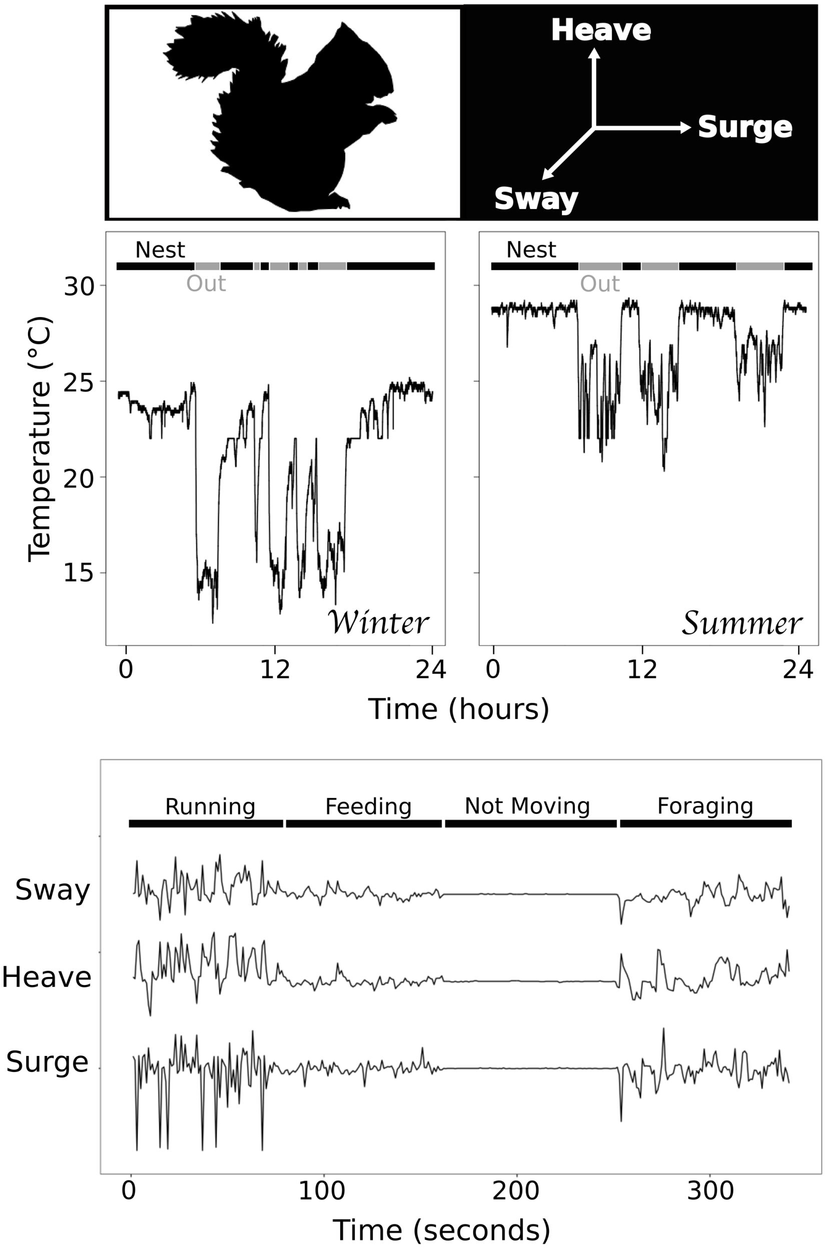

Figure 2.1 Example of temperature and acceleration biologger data on red squirrels demonstrating the distinct signatures of different behavioral states. This includes in (black bars) and out (grey bars) of the nest in the temperature data during both winter and summer, and running, feeding, not moving, and foraging signatures in acceleration data.

ecology of the species and which of these two temperatures vary more, collar temperature can be used to monitor thermal exposure (e.g., Osgodd & Weigl, 1972; Kanda et al., 2009) or heterothermic fluctuations indicative of torpor expression or hibernation (Lazerte & Kramer, 2016). Most pertinent here, collar temperature likely offers useful information about behavioral state, as it tends to more closely approximate the body temperature of inactive animals confined in small spaces (e.g. thermal refuges) and to more closely approximate the air temperature experienced by active animals fully exposed to ambient conditions (e.g., Messier et al., 1994; Körtner & Geiser, 2000; Murray & Smith, 2012; Wassmer & Refinetti, 2016; Olson et al., 2017).

An ideal candidate for investigating the potential for low frequency recordings is the North American red squirrel (*Tamiasciurus hudsonicus*), as their small size (~250g) drastically restricts potential battery life of biologging devices. This diurnal homeotherm uses insulated nests during rest periods, and remains active year-round (Humphries et al., 2005; Guillemette et al., 2009). In the northern boreal forest, they larder hoard resources every autumn to sustain activity and reproduction during the winter, resulting in large variation in activity and energy expenditure throughout the year (Humphries et al., 2005; McAdam et al., 2007; Fletcher et al., 2013). Due to the fact that they are diurnal, and actively defend small (0.3 ha) territories (Smith, 1968; LaMontagne et al., 2013), individuals are relatively easy to capture and observe in the wild.

Here, we used a combination of low frequency (1 Hz) acceleration and temperature recordings on free-ranging red squirrels to develop methods for biologger-based behavioral classification. Our main objective was to determine if accurate classifications can be achieved using low frequency accelerometer and temperature recordings from a small animal, and determine what modifications to common recommendations for behavioral classification methods of accelerometer data would be needed. The first part of our analysis develops a method that integrates temperature data into the behavioral classification allowing for identification of whether or not the individual is in a thermal refuge or not. The second part of our analysis explores different analytical approaches to the accelerometer classification to determine best practices for low frequency data. We initially complete the classification using the commonly used random forest approach, and use this to explore how selection of sample window size can affect both the accuracy of the classification and structure of the resulting behavioral dataset. Using this information on sample window size, we then manually create a hierarchical decision tree that starts with the broadest classification of behavior (2-behavior: not moving, moving) and then expands in detail with each subsequent branch until a 6-behavior classification is reached (see Table 2.1 for description of each stage). This approach creates a tree that can be easily clipped for the level of detail that is desired for different ecological questions. Finally, we compare the accuracy of the classification using the random forest algorithm to that of our manually created decision tree. This study demonstrates that manually created decision trees give a greater level of understanding and control over the classification, and allows adjustment of sampling windows to the characteristics of naturally occurring behavior. We show how to achieve accurate behavioral classifications on free-ranging small animals using low frequency accelerometer recordings and conclude by highlighting some of the difficulties that may be faced when trying to implement this method on other free ranging species, as well as how best to overcome them.

Materials and Methods

Study site and species

Between February and October 2014, we studied free ranging North American red squirrels in southwestern Yukon (61°N, 138°W), a population that has been part of a long term study since 1987 (McAdam et al., 2007). Male squirrels were trapped on their territories using Tomahawk live traps baited with peanut butter, and fitted with a collar (total weight = 8 g) combining a ventrally-mounted VHF radio-transmitter (model PD-2C, 4 g [1.7 % of body mass], Holohil Systems Limited, Carp, Ontario, Canada) and a dorsally-mounted tri-axial accelerometer (model Axy2, 4 g [1.7 % of body mass], Technosmart Europe). Accelerometers were set to record forces between -8 and 8 g_{force} at 1 Hz. Collars were constructed in the field on day of deployment (see Supporting Information 7.2.1). Once collared, squirrels were released and remained free-ranging, including during focal observations (see below), until they were recaptured an average of 22 days (range 5- 65) later and collars were removed. During 2014, we deployed 37 accelerometers on 20 individual red squirrels in winter (February) and mating season (March), 25 accelerometers on 18 individuals in summer, and 30 accelerometers on 30 individuals in autumn for a total of 1924 days of recordings.

Behavioral observations and scoring

We used two methods to record instantaneous behavioral states of free ranging red squirrels. In winter 2014, we located individuals using VHF and continuously recorded behavior for 2 min using an application built for iPod touch (see Supporting Information 7.2.2). Six behavioral states were recorded: feeding, not moving, in nest, running, slow travel, and stationary movement (defined as not travelling but still moving: e.g. grooming, vocalizing).

In autumn 2014, in addition to recording continuous behavior on the iPod app, we located individuals and recorded behavior with a video camera (Sony Handycam HDR-CX240) for as long as the individual was visible. Videos were watched by two observers and scored in real time, recording the start and end time of each behavior. Autumn behavior was categorized as: caching, clipping cones, digging, feeding, grooming, running, slow travel, and vocalizing. For all analyses, observed behavior were then combined into in nest, not moving, feeding, foraging (caching, clipping cones, digging, slow travel), stationary movement (grooming, vocalization), and travelling (see Supporting Information 7.2.6 for video). Over both winter and autumn deployments, we completed 1165 two-min observations on 20 individuals, and video-recorded a total of 83.8 h of direct observation on 27 individuals with videos ranging from 15 s to 12 min in duration.

Adjusting for time errors

Although we made every effort to ensure that accelerometers and time devices used for behavioral observations were synchronized upon deployment, the internal clocks on the different devices did not run precisely at the same rate. This resulted in small deviations, in the order of seconds, that would not be noticed if only a single recording device was used. However, when trying to synchronize and cross-reference observations recorded by two devices, such as an accelerometer and a focal observation app, these small deviations were significant, especially because most recorded behavior lasted for only a few seconds. We corrected the time on the observations by aligning abrupt changes in acceleration with abrupt changes in observed movement data (resting to travelling, and vice versa) on the two devices (see Supporting

Information 7.2.3 for details). We removed from future analysis all squirrels for which there was not an abrupt change in the observed data during a given day (320 of 403 squirrel days), leaving 46 squirrel days (12 individuals; 378 min) from the winter and 37 squirrel days (18 individuals; 326 min) from the autumn observational periods in the analysis.

In nest vs. out of nest

Red squirrels spend considerable amounts of time in their nests, during which time they mostly rest. The first stage of our classification was to identify whether or not the individual was in a nest. The accelerometer units recorded temperature in addition to acceleration (Figure 2.1). Following a similar method used by Studd et al. (2016), we inferred nest-use based on the concept that the ambient temperature of the local environment (i.e. surrounding the squirrel) is warm and stable when in the nest, and cold and variable when out of the nest. Before analysis, all temperature data was smoothed to filter out erroneous recordings (see Supporting Information 7.2.4). For each day of recordings (12 pm – 12 pm), we used k-means clustering constrained to 2 clusters to determine a daily threshold temperature, above which a squirrel was considered to be in the nest (Studd et al., 2016). This threshold is unique to each squirrel and day to account for changes in nest insulation (Guillemette et al., 2009), orientation of collar, and daily ambient temperature. As there are some occasions when squirrels were observed to be active and out of the nest but the temperatures were above the threshold, possibly as a result of the individual sitting in the sun, we imposed an additional constraint using the squirrel's activity levels from the accelerometer data. We assumed that squirrels use nests primarily for resting and, therefore, should not be moving most of the time they are in the nest. Thus, we calculated the proportion of each nest bout that the squirrel was moving versus not moving (using the method below) and reclassified any nest bout where the ratio of moving to not moving was above 1, as being out of the nest.

Moving versus not moving

Prior to all accelerometer analysis, we separated the static acceleration from the dynamic acceleration by applying a running means smoothing function at a window of 91 seconds. Following methods proposed by Shepard et al. (2008) on selecting appropriate window size for the smoothing, we completed a sensitivity analysis of the window on the estimation of overall dynamic acceleration (see Supporting Information 7.2.5). Although body orientation and posture can be determined from the static acceleration, we only used the dynamic acceleration (raw acceleration minus smoothed acceleration) for all analysis.

The first level of classification of the accelerometer data was to determine when the squirrels were moving or not moving (Figure 2.2). In most deployments, accelerometers would be turned on, packaged, and then sat on a table for 30 min to 8 h prior to being deployed. We selected a 1000 s section during this time from 36 accelerometers (14 winter, 22 autumn deployments), and calculated the delta dynamic body acceleration (ΔDBA), defined as:

$$\Delta DBA = \sum_{i=1}^{t} \Delta a_{Xi} + \Delta a_{Yi} + \Delta a_{Zi}$$

where the change in dynamic acceleration ($\Delta\alpha$) for the surge (x), sway (y), and heave (z) axis is calculated for each recording and then summed across a sample window (t). From our data of devices sitting still, we selected the 99.9% quantile of these ΔDBA measurements at a sample window (defined as the # of consecutive acceleration records over which the statistic is calculated) of 14 s as the threshold (1.06 g_{force}; Figure 2.2), above which the device was considered to be moving and below which to be not moving.

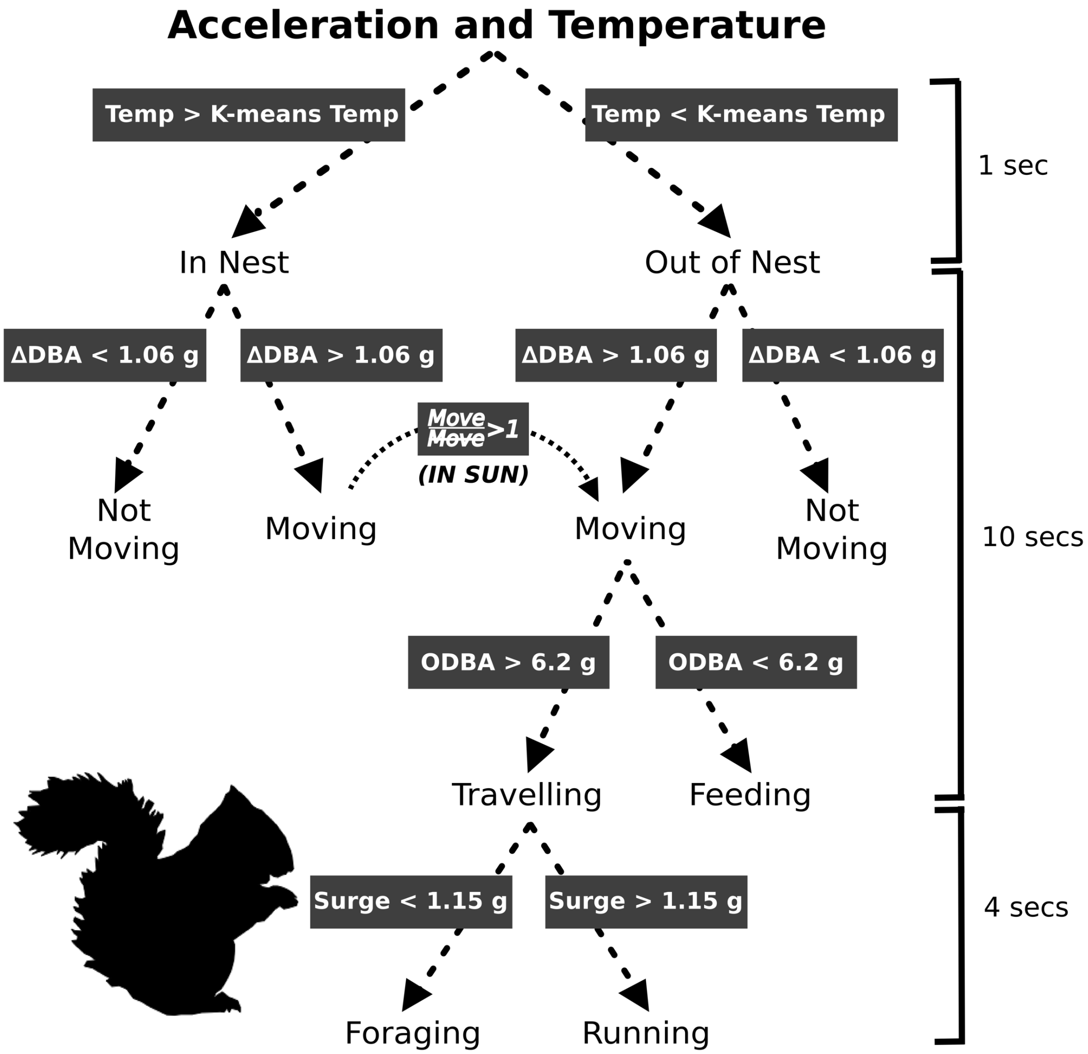

Figure 2.2 Classification decision tree of behavior from animal-borne acceleration and temperature biologgers on wild North American red squirrels. Red squirrel use of insulated nests can be identified through temperature signatures while behavioral state can be classified using acceleration. Classification was done at sample windows relevant to the natural duration of each behavior. For example, short duration behavior like running were classified at 4 second sample windows. Values in dark grey are the summary statistics and threshold values (in g_{force}) used for each division.

If moving: feeding versus foraging versus travelling

For the next stage of our hierarchical classification (Figure 2.2), we took all accelerometer data that indicated periods of movement and divided them into the three most common moving behavioral states (feeding, foraging, and running; 97.4% of observed movement). Using the random forest classification algorithm in R (Svetnik et al., 2003), we tested the degree to which accuracy of classification varied with the chosen sample window (2, 4, 7, 10, 14, 20, and 30 s). For this, we separated the focal observation data into segments of the desired sample windows, identified the most common behavior within these sample windows, calculated their duration, and selected only segments that met the following criteria: 100 % of sample window was feeding, at least 75 % was foraging with 0 % running, or at least 51 % was running (as running rarely continuously lasted for more than 4 s). To create our training dataset, we randomly sampled equal numbers of each behavior from this pool of segments. Across each window we calculated 6 summary statistics on the dynamic acceleration of each axis (mean, standard deviation, maximum, sum, range, and sum of $\Delta\alpha$), the overall dynamic body acceleration (ODBA; sum of the absolute values of dynamic acceleration; Wilson et al., 2006), ΔDBA, minimum $\Delta\alpha$, maximum $\Delta\alpha$, maximum acceleration, mean pitch, and mean roll using all three axes together for a total of 25 different summary statistics. All statistics were input into the random forest algorithm using 75% of observations for training (growing 2000 trees), and 25% for calculating the accuracy.

As an alternative method, we constructed a manual decision tree for classification using R (R Core Team, 2017). Our first division of moving behavior was into two categories: feeding and travelling. We selected a sample window of 10 s; we considered this sample window to be long enough that only the two behavioral states of interest would be relevant (those that naturally occur at that duration or longer). Following rationale suggested by Collins et al. (2015), we initially plotted histograms of all summary statistics for each behavioral category to visually determine which statistic had the clearest division between the two behavioral states (Figure 2.3). We then ran an optimization calculating the % error of classification of known behavior across a range of values of that statistic to determine a threshold value. This method is easily repeatable for separation of any behavioral states and was used to subsequently separate running from other forms of travelling (foraging), using only the segments of behavior that were correctly classified in the previous division. Since the average duration of running behavior in red squirrels is 4 s (see results), we ran this last division at a 4 s sample window.

Testing overall accuracy

Once our decision tree was built, we tested the accuracy in two ways: 1) at high resolution with the full observational dataset of detailed continuous behavioral observations used in the training as is commonly done in accelerometer calibrations (e.g., Bidder et al., 2014), and 2) at lower resolution with a 7 min behavioral observation data set that was collected concurrently during autumn 2014. We chose to test accuracy at two resolutions to explore whether issues with the time alignment may be influencing the accuracy values at the high resolution. These latter observations recorded behavior of each individual squirrel every 30 seconds for 7 min, as well as the occurrence of critical incidents defined as vocalizations, caching, and new feeding events. From these (n = 509), we selected only those 7 min observations where the individual spent 95% of the observations feeding (n=45), or travelling (n=50). For this analysis, travelling was defined as any combination of foraging and running as they always co-occurred over the course of 7 min. To eliminate issues of time alignment, we selected the inner 5 min of these observational periods

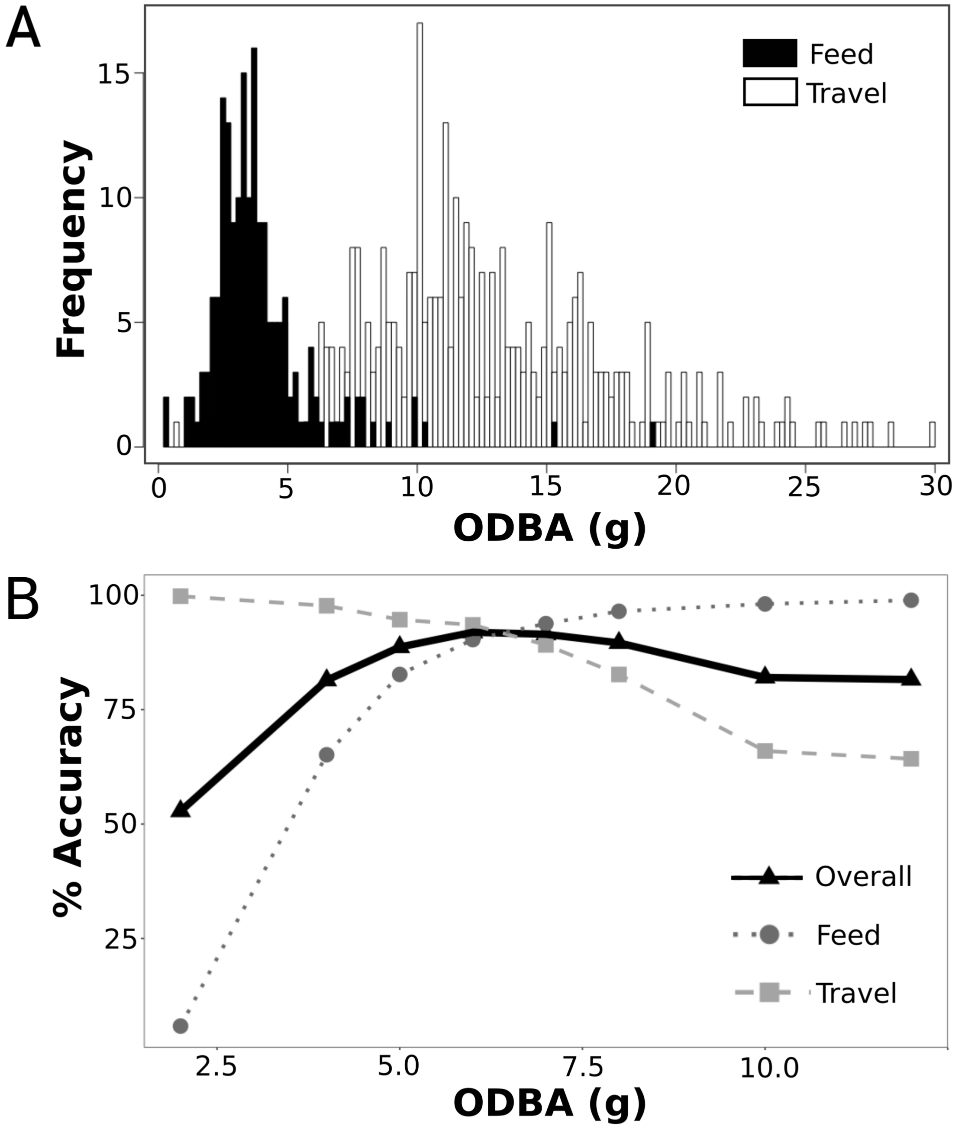

Figure 2.3 Example of methodology used for determination of threshold values in separating two behavioral states. Histograms of summary statistics were plotted to determine which statistics visually had the clearest distinction between two behavioral states (A). The optimal threshold value was then determined by assessing the accuracy of classification of each known behavior across the selected summary statistic (B). Here ODBA showed a clear division between red squirrel feeding and travelling (A) and an ODBA value of 6.2 g_{force} produced the highest overall accuracy (92.1%; B).

and tested whether the most common behavior from the accelerometer classification aligned with the most common behavior during those 5-min periods. To test accuracy of in/out of the nest for both accuracy measures, we assumed that since squirrels are diurnal and are known to sleep in nests, that the majority of each night all squirrels should be in nest. Thus, we randomly selected 400, 15-s samples between 10 pm and 4 am from accelerometers that were deployed during winter (n=200) and autumn 2014 (n=200) and labelled them as in nest. Accuracy was calculated for each step of the hierarchical decision tree (2, 4, 5, and 6-behavior classifications; Table 2.1) on a random subsample of 50 observational event for each behavior in the respected classification. We calculated the average accuracy and standard deviation for each behavior by repeating the subsampling process 100 times. Accuracy was calculated for the lower resolution behavioral dataset following the same method with the exception that: a) each subsampling selected 15 random observational events for each behavioral state due to lower total sample size, and b) only for the 5-behavior classification tree due to which behavioral states were recorded at this lower resolution.

Red squirrel seasonal time budgets

We calculated the average time budget per season for red squirrels using all accelerometer recordings used for the calibration. We selected a 10-day period in each season (winter: February 15 – 25, n=15; mating: March 10 – 20, n=9; summer: June 10 -20, n=12; autumn: Sept 5 – 15, n=24) and included all squirrels that had accelerometer recordings during that time. All recordings were converted to behavior using our decision tree (Figure 2.2), and the proportion of each day spent doing each behavior was calculated. To test if time budgets varied with season, we used a MANOVA analysis with a Pillai test in R (Fox & Weisberg, 2011) where the number of seconds per day spent doing each of 6 the behavioral states were the dependent variables, and season and squirrel id were the explanatory variables.

Results

In nest versus out of nest

Using a k-means cluster analysis to determine daily threshold temperatures for in/out of the nest and a movement-based correction, we achieved an overall nest classification accuracy of 91.6 ± 2.5%. The classification had higher accuracy for the out of nest (observed feeding, or travelling) category (93.8 ± 3.4%) than for the in nest category (89.3 ± 3.9%).

Moving and not moving classification (Two behavior level)

Before testing the accuracy of the moving/not moving threshold ($\Delta DBA = 1.06$), we removed all behavior classified as "in nest" from the testing dataset as we did not have visual confirmation of whether the individuals were moving or not while in the nest. On the remaining training data set of known behavior the threshold had an overall accuracy of 90.3 ± 2.3%. The accuracy of known not moving behavior was 83.9 ± 4.7%, and for known moving behavior was 96.9 ± 2.3%

Classifying moving behavior

We tested how different sampling windows influenced classification accuracy of the random forest machine learning algorithm. The overall accuracy increased with increasing sample window size from 84.8% correct classification at 2 seconds to 90.2% at 20 seconds before decreasing at the longest window size (Figure 2.4). The ability to distinguish feeding behavior was consistently above 90% for all sample windows increasing from 2 to 20 seconds. Foraging and running varied from 77% to 90.0% accuracy. However, using different sample window sizes influenced the average duration of each behavior classified through the analysis (Table 2.2).

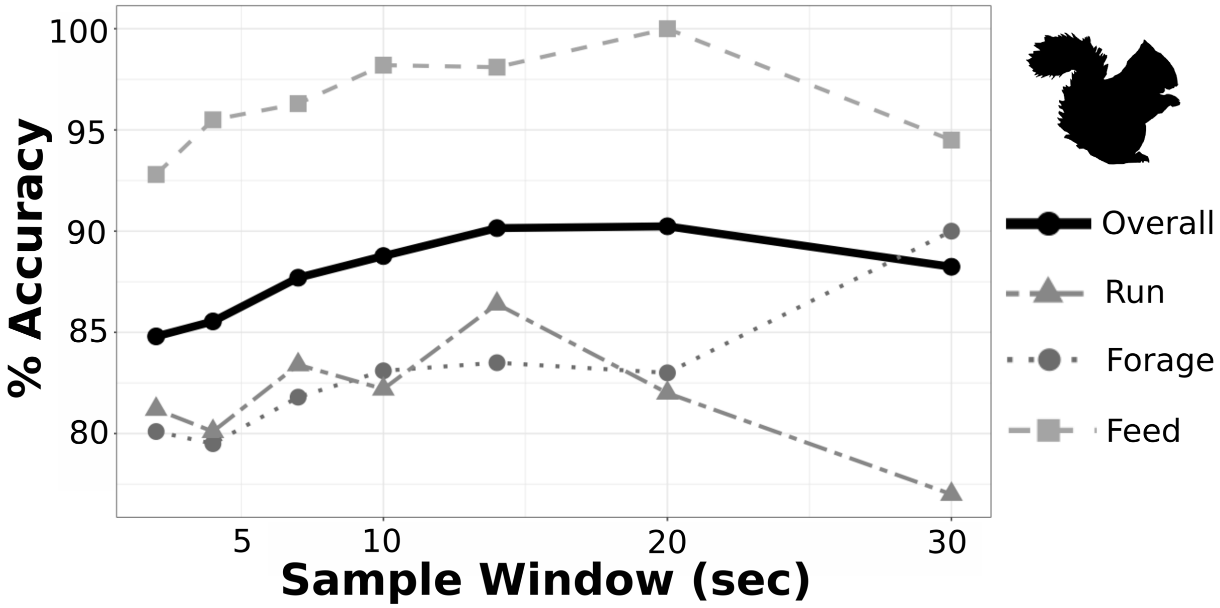

Figure 2.4 Percent accuracy of random forest algorithm at classifying accelerometer data to known active behavioral states at varying sample windows for red squirrels. Overall accuracy is the mean accuracy of the three behavioral states: running, foraging, and feeding.

The first step of the manual decision tree method was to separate feeding behavior (consumption of food) from travelling (foraging and running). We identified that ODBA provided the clearest division between the two categories. Optimization across a range of ODBA values produced the highest classification accuracy (92.1%) at a threshold of 6.2 g_{force} (Figure 2.4). Since the natural average duration of running was 4 seconds (Table 2.2), we selected that as our sample window to classify running from other travelling (foraging). We identified that the maximum value of the surge axis had the greatest distinction between the two behavioral states, although there was considerable overlap, with a threshold value of 1.15 g_{force} providing the highest overall accuracy of 71.9%, with individual accuracies of 78.0% and 65.9% of distinguishing foraging and running among the observations that had been classified as non-feeding behavior in the previous step of the decision tree (Figure 2.2).

Overall accuracy of decision tree

Accuracy decreased with increasing complexity of the decision tree where the highest accuracy occurred at the 2-behavior tree (91.6 ± 2.5%), and lowest accuracy at the 6-behavior tree (70.6 ± 2.3%; Table 2.3). For individual behavioral states, the accuracy was high for in nest (89.4 ± 4.2%), feed (86.3 ± 4.3%), and out of nest not moving (83.9 ± 4.7%), and low for foraging (66.4 ± 5.9%) and running (26.8 ± 5.8%). For these last two behavioral states, most error was associated with misclassification of running as foraging and vice versa as the combined category of the two behavioral states (travelling) had high accuracy of classification (89.4 ± 3.6%). Using an independent data set of 5 min observational periods, we were able to test the accuracy of the classification of feeding, travelling (foraging and running), and in nest behavior. The overall accuracy was 96.4 ± 1.7%, with individual accuracies of 97.8 ± 3.1% for feeding, 91.5 ± 6.9% for in nest, and 100 ± 0.0 % for travelling.

Seasonal time budgets

Red squirrels adjusted daily time budgets between seasons (MANOVA Pillai=1.25, F=70.0, df=15 and 1467, p<0.001), spending considerably more time in the nest not moving during winter (64.5 ± 0.7% of 24 hours) and mating season (56.5 ± 1.2%) than in summer (43.9 ± 0.8%) and autumn (36.4 ± 0.3%). Time spent foraging and running was the greatest during the autumn hoarding period (forage = 32.25 ± 0.3%, running = 7.9 ± 0.2%) and least during winter (forage =

5.7 ± 0.1%, running = 0.7 ± 0.0%), with intermediate amounts during summer (forage = 17.7 ± 0.3%, running = 3.6 ± 0.2%) and mating (forage = 10.9 ± 0.6%, running = 1.3 ± 0.7%). The amount of time spent feeding (autumn = 15.0 ± 0.2%, mating = 20.2 ± 0.6%, summer = 19.1 ± 0.3%, winter = 15.7 ± 0.02%), in nest moving (autumn = 4.1 ± 0.1%, mating = 6.1 ± 0.2%, summer = 5.5 ± 0.2%, winter = 7.6 ± 0.1%), and not moving (autumn = 4.4 ± 0.3%, mating = 4.8 ± 0.5%, summer = 10.3 ± 0.6%, winter = 5.7 ± 0.6%) were the most consistent behavioral states between seasons (Figure 2.5). These seasonal time budget differences were expressed consistently by most individuals across most seasons.

Discussion

We demonstrate that accurate behavioral calibrations are achievable using low frequency accelerometer recordings on free-ranging species with a decision tree methodology that is simple to use and easy to interpret. Our classification of 1 Hz acceleration and temperature recordings of red squirrels into 6 behavioral categories had an accuracy of 70.6%. However, classifying into 5 behavioral categories had a much improved accuracy of 87.5% in matching high resolution observational data and 96.4% accuracy in matching to the general behavioral state during 5 minute visual observations. This was the first terrestrial study, to our knowledge, that integrates acceleration with temperature, producing information on behavioral state as well as whether that behavioral state is expressed inside or outside of a thermal refuge. Using this calibration, we were able to produce the first seasonal time budgets for North American red squirrels, showing that there are substantial changes in daily behavior between seasons (Figure 2.5).

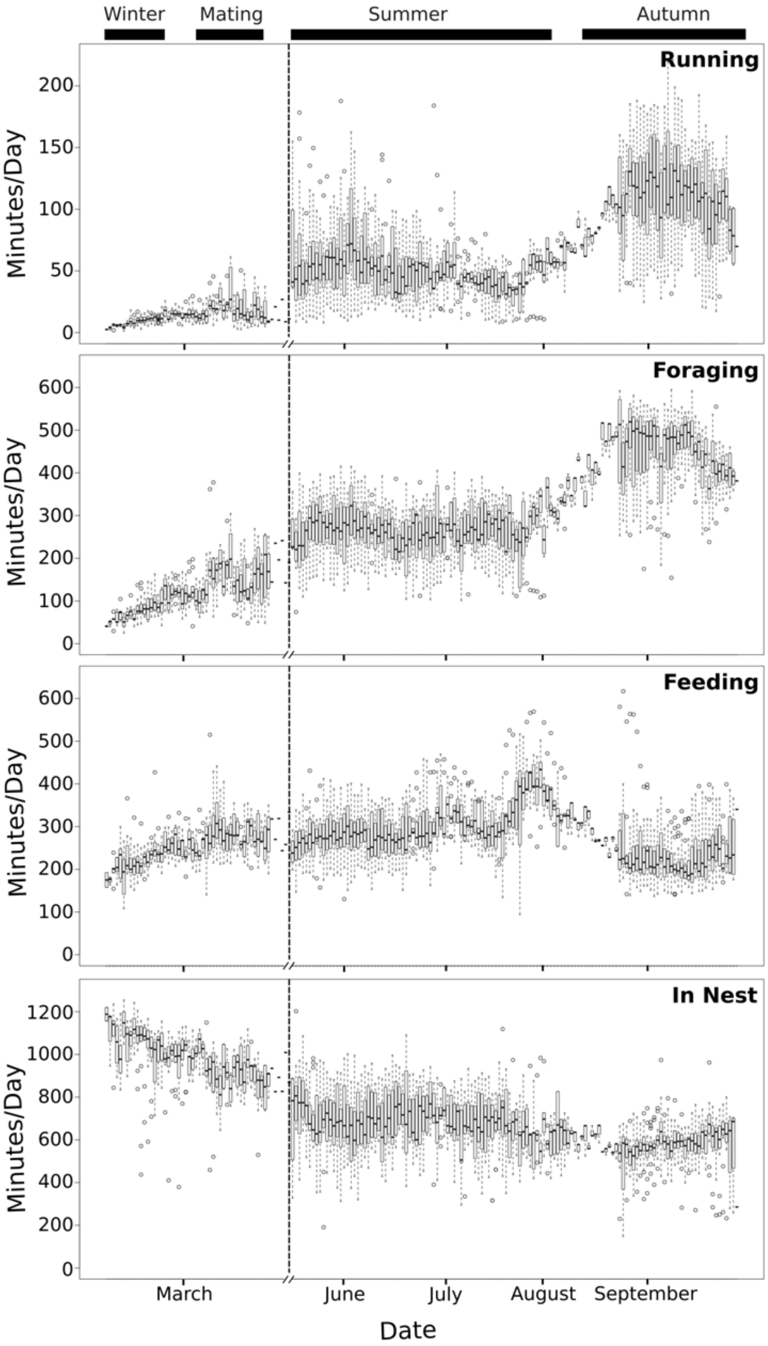

Figure 2.3 Time red squirrels spent each day from late winter to late autumn doing each of the four main behavioral states: running, foraging, feeding and in nest. Each box represents the interquartile range of all individuals as calculated from classified accelerometer data using a manual decision tree classification. The dotted line signifies a break in the time line when no accelerometers were deployed.

Here, we showed that the standard accelerometry practice of high frequency recording may not be as necessary as previously suggested. Our calibration of 1 Hz acceleration data yielded high overall accuracy while allowing continuous recordings on red squirrels for up to 2 months per deployment. This contrasts alternative methods of increasing sampling duration of these devices through non-continuous sampling regimes. For example, on chipmunks, Hammond et al. (2016) recorded at a commonly recommended 20 Hz which required a sampling regime of 10 seconds every 15 minutes in order to achieve a 4.5-day sampling period. If a continuous recording regime had been used, the maximum sampling period would have been just over one hour. While our study design (exclusive reliance on low frequency sampling) does not permit direct comparison of accuracies that could have been obtained with higher sampling rates, we can assess this indirectly by examining the classification accuracy of behavioral states of variable duration (see recommendation 2 below). However, future research on the direct comparison of sampling rate is warranted by subsampling a higher frequency recording while allowing for variation in sample window size with each new sampling rate (see recommendation 3 below). Currently all comparative studies that have been completed maintain the same sample window size for all recording frequencies (e.g., Wang et al., 2015; Pagano et al., 2017) which may be driving the sudden and drastic decrease in accuracy seen at low frequency recordings (Figure 2.4). Despite this, the accuracies that we achieved here (70.6% to 91.6%) were comparable to other studies which sampled at much higher rates (3.3 Hz to 40 Hz) with accuracies ranging from 75% to 98% (Nathan et al., 2012; Bidder et al., 2014; McClune et al., 2014; Hammond et al., 2016).

Our study is one of few that has completed a calibration using free-ranging individuals. Although many calibrations use captive animals or surrogate species for training data (Campbell et al., 2013), Pagano et al. (2017) showed that highest accuracy is achieved using free ranging individuals of the same species of interest. We followed this advice by incorporating observations from both low activity (winter) and high activity (autumn) seasons for training, attempting to incorporate the full range of potential movements that red squirrels might express in the calibration. Although specific behavioral states may change between seasons, at the broad behavioral categories that we were using, there was no evidence that there were distinct enough seasonal differences to merit a separate calibration for each season, but future research could explore this in more detail. The one aspect of the calibration that may be susceptible to seasonality is the use of temperature for determining in and out of the nest, where the efficacy depends on the nest temperature being distinctly warmer than ambient air temperature (Osgodd & Weigl, 1972). The population of red squirrels used in this study lives in a climate where this is always the case and even in summer we found that you could clearly distinguish between in and out of the nest (see Figure 2.1 for example), but this may not be the case in all studies. Despite the high accuracy that we achieved, we would like to highlight a couple issues that were encountered with both low frequency recordings and working on free ranging individuals that may be common to others who follow a similar methodology.

First, when recording at a lower frequency than the stride frequency of the species, some commonly used and recommended analytical techniques (spectral analysis, orientation; Brown et al., 2013) may become less applicable. At 1 Hz, the data recorded is a snapshot of acceleration values from each movement type. This means that it will not always record the peak acceleration that was reached but some value along the wave of accelerations experienced during each stride. Second, no two time devices will record time at precisely the same rate due to variation in crystal oscillating frequency in each time device, which is influenced by general noise, voltage change, temperature, and aging of the clock (Syed & Heinemann, 2006). When there is a need to precisely align instances recorded on two devices, for example to calibrate one observation method via another using instantaneous observations recorded every second or less, then small time offsets become noticeable and problematic. Until behavior and accelerometer data can be collected over a network with a shared clock, studies on free-ranging animals fitted with non-networked, store-on-board biologgers will face this problem (see Gaylord & Sanchez, 2014).

Although these two issues do make field-based calibrations of low frequency acceleration more difficult, they do not preclude detailed time budget classification and an overall assessment of classification accuracy. We conclude the paper with some recommendations for behavioral classifications using low frequency acceleration, applicable to a research context in which the priority is to accurately classify major behavioral states, recorded continuously, across a sampling period of maximum length.

1) **Behavioral observations used for calibrations should be continuous and as long in duration as is possible for the study species**. More stark transitions between behavioral states (travelling to not moving and vice versa) within each observational period makes it easier to accurately align events recorded on both devices. That being said, the feasibility of long duration, continuous observation sampling varies by species. Although red squirrels are relatively easy to observe, their small size, arboreality, and rapid movement, all within a three-dimensional visual obstructed forested landscape makes long continuous observations challenging to obtain. As a result, we had to remove 80% of observational periods (320 of 403 squirrel days) from the analysis because in too many instances we did not observe enough major

transitions within a single continuous bout to accurately and objectively align time as recorded by the accelerometer and the observer.

2) **Select behavioral states that naturally occur at durations longer than both the recording frequency, and the error in the time alignment**. Longer duration behavioral states provide the opportunity to select the middle segment of each occurrence, thereby eliminating the chance of working with mislabeled accelerometer data from misalignment. If classifying a behavior that typically lasts for 2 seconds, using a 1 Hz sampling rate with a 2 second error in alignment, the likelihood that the labelled segment will include the matching acceleration is only ~30%. We found that short duration behavior had the lowest accuracy (26.8%) when testing on observational data aligned to the second, a pattern that is common to other studies (e.g., Pagano et al., 2017). We used a lower resolution observational data set (five-minute) to test if the low accuracy is likely resulting from misalignment of time. If the inaccuracies are the result of poor ability of the decision tree than we would expect that accuracies would be similar between the low and high resolution datasets, while if the errors are stemming from time alignment then we would expect higher accuracy at the lower resolution when time misalignment has minimal effects. We found that accuracy of lower resolution data was ~10% greater than the higher resolution data, suggesting that our estimate of classification accuracy for short behavior is likely more conservative than is actually the case. Though this is vaguely reassuring, accurate classification (and assessment of classification accuracy) becomes an increasingly intractable challenge as behavioral duration begins to approximate sampling rate. The trade-off between sampling rate and sampling duration dictated by the accelerometer manifests as the same trade-off affecting the behavioral classification. Extending the sampling duration by reducing the sampling frequency inevitably compromises detection of behavioral events confined to very

short time intervals. Thus, researchers will need to set expectations to either accurately documenting fine scale behavior continuously at millisecond sampling rates, or accurately documenting long-term behavior continuously over months and years, as likely both, at the same time, with the same device will not be possible.

3) **Create classifications using a manual decision tree.** There are two key benefits to this approach over a machine learning algorithm. First, creation of hierarchical decision trees become possible, such that classification can be performed at multiple levels of complexity, starting with coarse distinctions (e.g., active vs. inactive) that subdivide into more resolved categories (e.g., active subdividing into different types of activity) (Figure 2.2; e.g. McClune et al., 2014). This allows for a tree that can be easily trimmed post calibration to match the ecological question being studied that has an accompanying accuracy for each trimming. For example, if a study is only interested in when the animal is vigilant versus active when out of the nest, the tree can be trimmed to four behavioral states (moving/not moving) with the knowledge that the accuracy is 90.3%. Second, this provides an opportunity to classify each step separately starting with the longest duration behavior for which the time alignment issue should be trivial, and proceeding towards the shortest duration behavior. Data can be cleaned at each stage ensuring that when distinguishing the shortest duration behavior, the training dataset has the lowest error due to time alignment.

4) Select sample windows based on the duration characteristics of the behavior, and the recording frequency. Sample windows must be large enough to contain multiple samples of acceleration in order to calculate the summary statistics. Generally, calibrations of high frequency recordings use sample windows of 1 to 2 seconds (20 to 80 samples, e.g. Pagano et al., 2017). Using lower recording frequencies require larger windows, and thus run the risk of extending beyond the natural duration of the behavior being classified. Although, it may always be possible to find a summary statistic that can separate two behavioral states at any sample window (Figure 2.4), selecting an inappropriate window will result in unrealistic behavioral durations (Table 2.2) leading to biased time budgets (Robson & Mansfield, 2014). Thus, it is critical that careful consideration is given to sample window size, and it may be necessary to incorporate different sized windows for different behavioral categories into the classification, as we did in this study (Figure 2.2).

5) Select summary statistics that are consistent across individuals. Variation in the placement of accelerometer tags during attachment to each individual may influence deployment angles and what each axis is actually measuring. In our study, despite the fact that all tags were attached in the same orientation on all individuals, the nature and weight balance of the collars resulted in the devices spinning around the neck of the animal and resting in unique orientations for each individual. One option to counteract this problem during calibration is to do individual-specific calibrations, when possible. The other option is to carefully select summary statistics for the calibration that will not be influenced by this issue, such as statistics that are summaries off all three axis (e.g. ODBA, ΔDBA), or single-axis values that are not affected by the possible range in deployment angles (e.g., surge axis in our study).

Accelerometers provide an unprecedented potential for ecologists to estimate time- and energy-budgets of many species at a level of detail that is not achievable by traditional methods. We found that the limitations in the applicability of these devices on small species can be alleviated through low frequency recordings without loss in accuracy, though low sampling rates do preclude the detection of very short behavior. With an ability to record behavior continuously on small species regardless of light or weather conditions, ecologists can now not only explore time budgets at seasonal scales as we did here (Figure 2.5), but also how the timing of behavior is structured throughout a day (Ropert-Coudert et al., 2004). Having access to this detail provides a means for easily incorporating behavioral responses of species to their environments into broader and more complex questions about how they may interact with the species around them in a changing world.

Data Accessibility Statement

All data from this study is archived on Dryad (doi:10.5061/dryad.1s1m8r7).

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Table 2.1 - Definitions of each behavioral category used in each step of the hierarchical decision tree completed in this study. Table illustrates how each subsequent behavioral state is nested within a category in a less complex tree.

2-Behavior		**4-Behavior**		**5-Behavior**		**6-Behavior**	
Category	**Def.**	**Category**	**Def.**	**Category**	**Def.**	**Category**	**Def.**
Out of Nest	Outside a thermal refuge.	**Moving**	Outside a thermal refuge and some part of the animal is moving.	**Travelling**	Animal is moving in space at either a slow or fast locomotion state.	**Foraging**	Slow locomotion consistent with searching for and collecting food.
						Running	Fast locomotion consisting of more than 1 stride at a time.
				Feeding	Not moving in space but body is moving with the handling and ingesting of food.		
		Not Moving	Outside a thermal refuge and no part of the animal is moving except for breathing.				
In Nest	Inside a thermal refuge.	**Moving**	Inside a thermal refuge and some part of the animal is moving.				
		Not Moving	Inside a thermal refuge and no part of the animal is moving except for breathing.				

Table 2.2 - Average durations in seconds of each behavior common in red squirrels calculated from different classification methods. Winter and autumn durations are tabulated from observations of free ranging squirrels during each season (winter: 18 squirrels, 2328 min; autumn: 27 squirrels, 621 min). These are compared to durations calculated from classified accelerometer data from 6 squirrels (3 winter, 3 autumn) using the random forest method with varying sample sizes of 2 – 30 seconds, and a manual decision tree method (DT).

	Observed		**Predicted - Random Forest**							
	Winter	Autumn	2	4	7	10	14	20	30	**DT**
Feed	45.89	24.03	3.84	20.24	32.1	48.5	54.5	72.49	81.61	57.75
Forage	8.29	10.56	3.22	8.02	13.07	18.43	23.86	32.69	58.33	19.01
Run	5.2	3.77	3.78	11.82	19.74	28.98	42.94	66.05	60.47	7.44

Table 2.3 - Mean percent accuracy of the manually-created decision tree at correctly classifying each behavioral state in four trees of increasing complexity. Mean accuracy is calculated over 100 subsampling events of observational data (50 observations per behavioral state). There is no observational data of whether red squirrels were moving or not moving while in the nest so those two categories were combined as 'In Nest' for the 4, 5, and 6-behavior classification trees.

2-Behavior		**4-Behavior**		**5-Behavior**		**6-Behavior**	
Category	Mean ± sd	Category	Mean ± sd	Category	Mean ± sd	Category	Mean ± sd
Out of Nest	93.8 ± 3.4%	Moving	96.9 ± 2.3%	Feeding	86.7 ± 4.0%	Feeding	86.3 ± 4.3%
				Travelling	89.4 ± 3.6%	Foraging	66.4 ± 5.9%
						Running	26.8 ± 5.8%
		Not Moving	83.9 ± 4.7%	Not Moving	84.2 ± 4.6%	Not Moving	83.9 ± 4.7%
In Nest	89.3 ± 3.9%	In Nest	90.0 ± 4.1%	In Nest	89.8 ± 4.2%	In Nest	89.4 ± 4.2%
Total	**91.6 ± 2.5%**	**Total**	**90.3 ± 2.3%**	**Total**	**87.5 ± 1.9%**	**Total**	**70.6 ± 2.3%**

Linking Statement

In the previous chapter, I developed methodological approaches for the use of low-frequency acceleration and temperature data to record behaviour continuously for long durations (weeks to months) on small mammals. The classification used requires direct observations for training data that is sometimes not easy to collect on free-ranging species. In the next chapter, I test the same classification methodology on snowshoe hares, but due to the hare's cryptic nature and an inability to observe individuals in the wild, I also test the applicability of using acoustic recorders for capturing behaviour. As a case study to highlight the application of these devices to studying animal behaviour, this chapter also investigates behavioural responses of snowshoe hares to changing moonlight conditions.

Chapter 3 - Use of acceleration and acoustics to classify behavior, generate time budgets, and evaluate responses to moonlight in free-ranging snowshoe hares

Abstract

Technological miniaturization is driving a biologging revolution that is producing detailed and sophisticated techniques of assessing individual behavioral responses to environmental conditions. Among the many advancements this revolution has brought is an ability to record behavioral responses of nocturnal, free-ranging species. Here, we combine captive validations of acceleration signatures with acoustic recordings from free-ranging individuals to classify behavior at two resolutions. Combining these classifications with ~2 month-long recordings, we describe winter time budgets, and responses of free-ranging snowshoe hares to changing moonlight. We successfully classified snowshoe hare behavior into four categories (not moving, foraging, hopping, and sprinting) using low frequency accelerometry, with an overall model accuracy of 88%, and acoustic recordings to three categories (silence, hopping, and chewing) with an accuracy of 94%. Broad-scale accelerometer-classified categories were composed of multiple fine-scale behavioral states with the composition varying between individuals and across the day. Time budgets revealed that hares spent ~50% of their time foraging and ~50% not moving, with most foraging and feeding occurring at night. We found that hares adjusted timing of activity in response to moon phase, with a 6% reduction in foraging and 30% reduction in travelling during the night when the moon was full. Hares compensated for this lost foraging time by extending foraging into the morning hours of the following day. Using two biologging technologies to identify behavior, we demonstrate the possibility of combining multiple devices when documenting behavior of cryptic species.

Introduction

From satellites and drones to biologging devices, new technologies are providing us with the capabilities to answer questions about the natural world, and the species that live within it that could only have been dreamt about a few decades ago. Every year, the number of technologies available to ecologists expands, and the sophistication and capacity of those tools that exist improves (see reviews: Elliott, 2016; Williams et al., 2016). Although initial incorporation of devices on wildlife focused on space use, with a focus on knowing in real time the exact location of an individual, the latest phase of the biologging revolution has, in part, been behaviorally focused, with a desire to know what the individual was doing (Wilmers et al., 2015). One of the most popular devices for behavioral classification is the accelerometer, which measures 3-dimensional acceleration of a species of interest (see Figure 3.1; e.g., Graf et al., 2015) and for which miniaturization has reduced the weight to as little as 0.7 grams (e.g., Axy-4 without battery, Technosmart, Rome, Italy). Taking into account gravity and acceleration profiles of different movement types, these recordings can provide information on posture and orientation, energy expenditure, and activity levels, that should correspond to specific behavioral states (Wilson et al., 2006; Shepard et al., 2008; Gleiss et al., 2011; Brown et al., 2013).

The potential for accelerometers to record behavior over long timeframes, including multi-day, cross-seasonal, and even multi-annual periods, involves a tradeoff between recording duration and the resolution of behavioral classification (Broell et al., 2013; Tatler et al., 2018). Accurate classification of detailed behavioral states requires a sampling rate that is twice the highest frequency present in the signal, referred to as the Nyquist criterion (Beutler, 1966; Chen & Bassett, 2005; Graf et al., 2015). Most classifications target rapid movements like wingbeats or

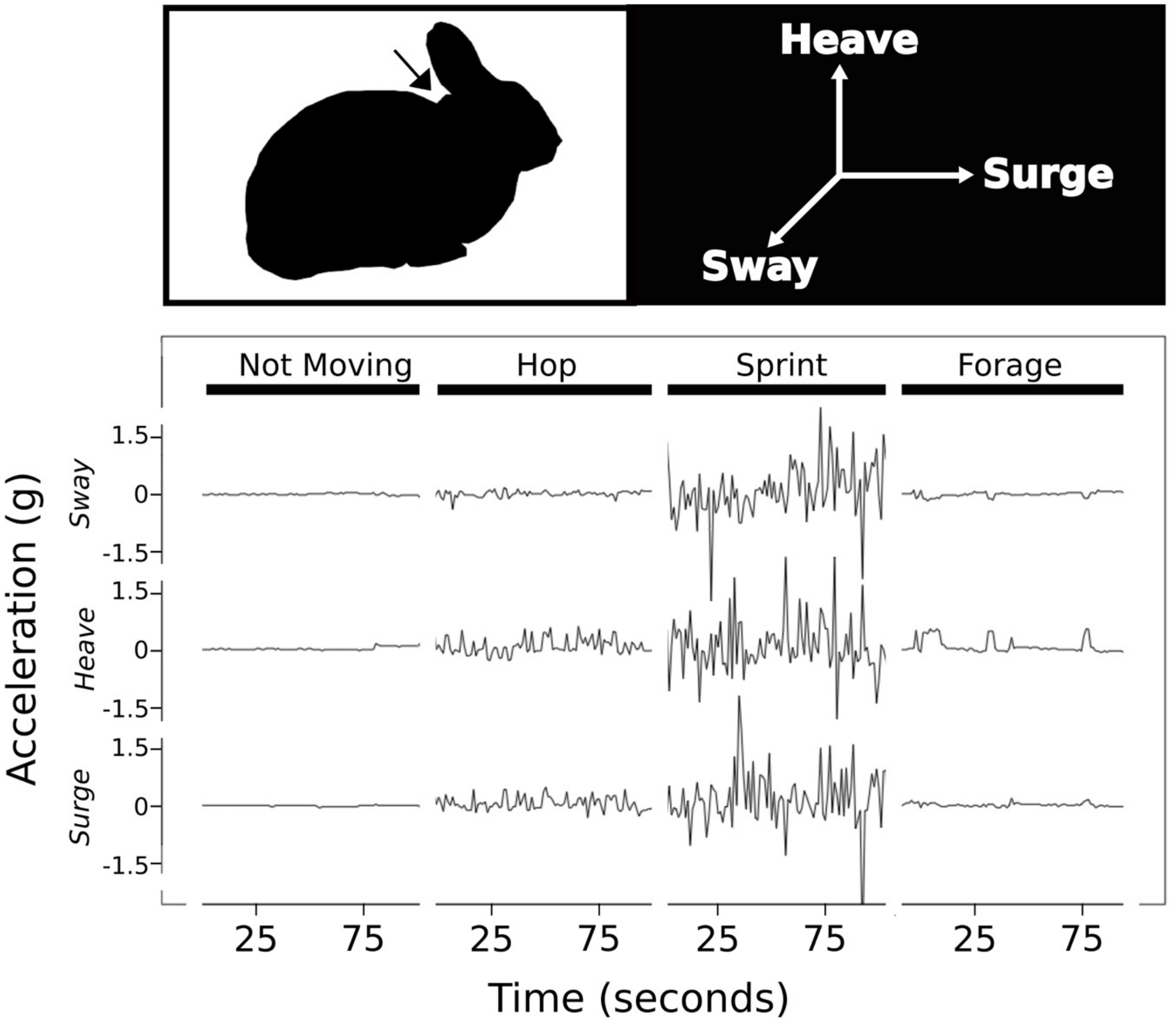

Figure 3.1 Example of 1Hz tri-axis accelerometer data and the orientation axis from a collar attached to a captive snowshoe hare. Arrow indicates location where accelerometer rested on the animal.

steps (Shepard et al., 2008; Spivey & Bishop, 2013), but the intensive sampling needed to do so tends to limit device longevity below what is necessary for documenting wildlife responses to changes in their environment that occur at seasonal and annual timescales. To increase recording duration, sampling frequency can be lowered at the cost of only capturing behavioral categories with lower Nyquist criterion such as bouts of travelling, foraging, and resting (Campbell et al., 2013; Tatler et al., 2018; Studd et al., 2019). Such information, although less specific, is still highly useful for building activity and energy budgets (Williams et al., 2017; Studd et al., 2019).

To counteract the loss of information from using a lower sampling frequency, it may be necessary to determine the detailed behavioral composition of the broader behavioral categories through different means. In species where direct observations are difficult, this may require combining accelerometers with additional biologging technology such as video or audio recorders (Lynch et al., 2013; Pagano et al., 2018). For large terrestrial species (such as polar bears and caribou), observational data on free-ranging behavior can be obtained with video camera collars (e.g., Thompson et al., 2012; Pagano et al., 2018), while for smaller taxa where weight of monitoring devices becomes limiting, deployment of acoustic recorders may be a potential alternative (Lynch et al., 2013; Couchoux et al., 2015). Acoustic data has been incorporated into many fields within ecology providing new means of quantifying biodiversity (e.g., Depraetere et al., 2012; Gasc et al., 2013), soundscapes (Pijanowski et al., 2011) and animal communication (e.g., Reby & McComb, 2003; Fischer et al., 2004; Thiebault et al., 2016). More recently, a few studies have even revealed the potential of acoustic devices to record non-vocal behavior (e.g., flying, feeding, walking; Ilany et al., 2013; Lynch et al., 2013; Stowell et al., 2017; Wijers et al., 2018).

Here we highlight the potential of using accelerometers and acoustic recorders (attached as collars) to classify the behavior of free-ranging snowshoe hares (*Lepus americanus*), a cryptic small mammal (2kg). Our primary objective was to determine if we could use low frequency acceleration to identify broad behavioral categories that could be recorded over days to months.

In order to do this, we linked accelerometer recordings to observations of captive hares. Additionally, we took advantage of the ability of acoustic recorders to classify non-vocal behavior in order to determine a more detailed composition of accelerometer-based behavioral categories. Our secondary objective was to showcase how these tools, in providing detailed behavioral information over long periods of time, can then be used to investigate daily activity patterns and how aspects of the environment can influence behavior of free-ranging hares. We took a proof of concept approach whereby we explored how light conditions caused by phases of the moon and daylight influenced nocturnal hare behavior.

Materials and Methods

The study took place in southwestern Yukon (61°N, 138°W) within the Shakwak trench, an area of boreal forest where snowshoe hares have been the focus of studies for the past 45 years (Krebs et al., 2018). The forest is predominantly white spruce (*Picea glauca*) intermixed with patches of aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*), and an understory of gray willow (*Salix glauca*) and dwarf birch (*Betula pumila var. glandulifera*) (Boonstra et al., 2016). Snowshoe hares exhibit 10-year population cycles, which are, at least in part driven by their primary predators Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), and great horned owls (*Bubo virginianus;* Rohner & Krebs, 1996; O'Donoghue et al., 1998). During this study, snowshoe hares were in the increase phase of the cycle with densities averaging 1 hare/ha (Krebs unpublished).

All snowshoe hares were captured using Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) baited with alfalfa and rabbit chow, and set and checked overnight (Keith, 1964). Individuals were fitted with an accelerometer (model Axy3, 4 g, Technosmart, Rome, Italy) and VHF radio transmitter (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada, both 27g +/- 1g) in the form of a collar (31g +/- 1g, 2.5% of smallest hare mass). Accelerometers rested on the dorsal side of the neck and recorded acceleration on 3 dimensional axes at 1 Hz with a resolution of +/- 8 $\mathrm{g}_{\text{-forces}}$. To record observations of snowshoe hare behavior, we captured six hares (>1200g) in April 2015, attached collars and transferred them to outdoor enclosures (4.5m by 4.5m; modified from Sheriff et al., 2009; Lavergne and Boonstra pers comm). Hares were held for three days and supplied with rabbit chow, water, and willow branches collected from the surrounding area. At the completion of observational trials, collars were removed, and hares were released at point of capture. To explore the potential of accelerometers for monitoring behavior over multiple months, we live-trapped and collared 14 free-ranging snowshoe hares between October 2015 and March 2016. Once collared, hares were released at their capture site, and recaptured 1-3 months later (average=62 days, range: 32-100 days) for collar removal and data download. This research conformed to the guidelines of the American Society of Mammalogists (Sikes, 2016) and was approved by the McGill University, University of Alberta, and University of Toronto Animal Care and Use Committees.

Behavioral observations of captive and chased hare

We used the observations of captive hares to cross-validate behavioral categories based on accelerometer information. For this, two hours of video (Nikon D90 with 50mm, Sony Handycam HDR-CX240) were recorded per day for three days capturing morning and dusk activity. During recordings, personnel left the enclosure area to minimize influence of human activity on hare behavior. Hares tended to move rapidly when humans entered the enclosures to provide food and remove droppings, so cameras also recorded during these times. The same time-keeping device was held in frame at the start of each video to sync times for all observations. Videos were watched by two observers who recorded the start and end times of each behavior, which included digging, feeding, grooming, jumping, vigilance (sitting while head moves to look in multiple directions), sprinting, shaking, sitting (motionless), standing, travel with multiple hops, or travel with one hop only. From this we selected the six most common behavioral states that represented 91.8% of all observations and combined them into three broader categories (not moving: sitting and vigilance; foraging: feeding and travel with one hop; travelling: sprinting and travel with multiple hops). This included at least one observation of each behavior per hare per day with the average number of observations of each behavior per hare per day ranging from 8 for feeding to 42 for vigilance (supplementary materials Table S7.3.1). Since clocks on separate devices did not run at exactly the same rate, we visually identified multiple occasions per day per hare where the animal transitioned from sitting to travelling to calculate the time divergence between each accelerometer and the camera clock to generate a time correction equation for each accelerometer (error = +/- 3 sec).

We observed few instances of hares sprinting at maximum speeds in the enclosures. Thus, to capture potential high-speed chase or ‘fleeing’ behavior (an important aspect of predator-prey interactions), we added additional behavioral data from free-ranging snowshoe hares that were chased by a simulated predator (i.e., a dog, *Canis familiaris*, a model for coyotes; see methods in Boudreau et al., submitted). For each chase, the time and whether or not the hare sprinted were recorded, and a subset of chases (n=47) where hares were observed sprinting from the dog were used as examples of sprinting behavior.

Accelerometer classification

Average static acceleration was calculated using a running medians smoothing window of 91 samples (see supplementary materials 7.3.1 for window size selection method). We removed this long duration static acceleration (general orientation of device) from total acceleration to retain only acceleration generated from the movement of the animal on which all further analyses were based. This remaining acceleration is primarily the measurement of small changes in the posture of the animal that occur during each behavior, and secondarily, measurements of the dynamic acceleration of the movement. To classify acceleration by behavioral categories we constructed a decision tree consisting of three hierarchical divisions (Studd et al., 2019): 1) not moving (no visible motion, i.e. sitting) and moving (any physical movement), 2) all moving into foraging (feeding, travel with one hop) or travelling (travel with multiple hops), and 3) all travelling into hopping (observed in enclosure) and sprinting (observed in simulated chases in the wild). For each division of the tree, observed behavioral data was split between training (70%) and testing (30%), and then subsampled to ensure equal numbers of each behavior. Over each sample window duration, determined by the average duration observed in videos of behavioral states in each division, we calculated the mean, maximum, minimum, range, standard deviation, and sum of acceleration on each of the three axes (surge, heave, and sway), along with the sum of overall acceleration (OA; similar to ODBA in Wilson et al., 2006), and the change in overall acceleration (ΔOA) across all three axes. ΔOA is the change in acceleration ($\Delta\alpha$) for each axis from one second to the next summed over the time window across all three axes. Threshold values for behavioral categories at each division were determined by a two-step process. First, the percent overlap between the two behavioral categories for each summary statistic was calculated and the statistic with the lowest overlap was selected (Figure 3.2a). Second, the percent error of classification was calculated for every 0.1 increment of the selected statistic between the minimum and maximum values, and the threshold value was set according to the lowest classification error (Figure 3.2b). Using the remaining 30% of the observational data, accuracy for each division of the tree was calculated as proportion of all observations that were correctly classified by the threshold value.

The flexibility of this method allows for different sample duration windows to be used at each division. Sample window size was 12 second for not moving and moving, and 4 sec for each of foraging and travelling, and for hopping and sprinting. Different training datasets were used for each division. For the first division we used all not moving and moving events with durations of at least 12 seconds (91.8% of observed behavior). The second division included all foraging (51% or more feeding with no type of travel) and travelling (51% or more travel with multiple hops) events that lasted at least 4 seconds (89.4% of observed behavior). The final division included all hopping (low speed travel with multiple hops) and sprinting (simulated predator chases) events with summary statistics calculated over 4 seconds. Due to low sample size of sprinting events, overall classification accuracy was calculated on the first two divisions only.

Although we used a threshold-based classification approach, much recent accelerometer-based literature uses alternative machine learning methods. These approaches have the advantage of efficient processing for the generation of complex classifications with high accuracies, but the disadvantage of black box, non-transferrable thresholds and non-hierarchical trees (Bidder et al., 2014; McClune et al., 2014). Given pros and cons to both approaches, we also explored the

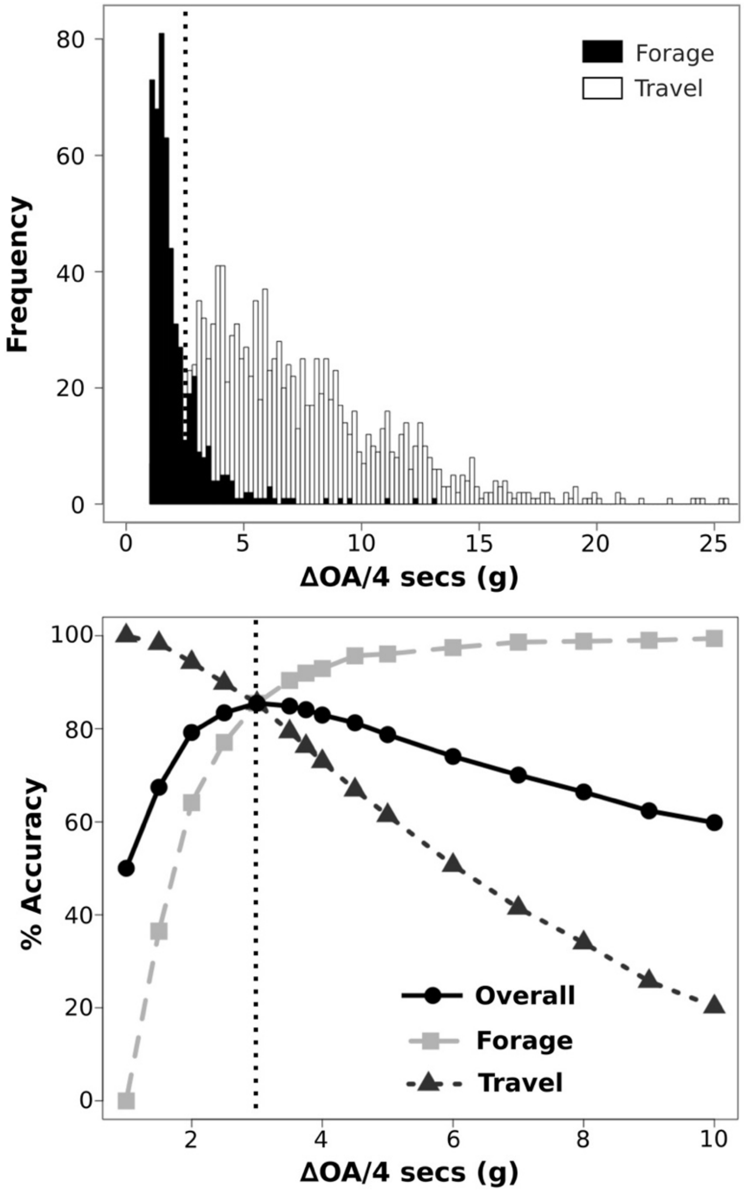

Figure 3.2 Example illustrating method for determination of threshold values for separation of behavioral states using accelerometer data from collars attached to snowshoe hares. Histograms provide visualization of percent overlap between two behavioral categories using a given summary statistic (A). Optimization is performed by examining the accuracy of the behavioral classification between two behavioral states across a range of values and selecting the value at which the overall accuracy is the highest and where the individual accuracy of each behavior intersects. Dotted line represents the selected threshold value for classifying accelerometer data into forage and travel using ΔOA.

accuracy of random forest-based classification, as described more fully in the supplementary materials (see 7.3.2), and briefly describe the outcome of this alternative approach in the results. As the random forest provided similar results, we decided to report the more simple method in the body of the paper.

Using acoustic recorders to refine accelerometer-classified behavior

We used animal-borne acoustic recorders to explore composition of broad behavioral classifications (i.e. not moving, and foraging) generated from our low frequency accelerometer recordings. In January 2018, we captured three male snowshoes hares and fitted them with an accelerometer-VHF combination collar that contained an acoustic recorder (Edic-mini Tiny+ A77, 6.6 g, total collar weight of 41g, <3% of body mass). Once collared, each individual was released at the capture site and recaptured between 4 and 22 days later. Audio recorded continuously at 16000hz with μ-law compression for three days following capture. Prior to acoustic analysis, we listened to and recorded the sounds contained within 135-15 second audio clips (45 per recorder) that corresponded to long duration (>15 sec) foraging, not moving, and travelling as determined by our accelerometer classification tree. Listeners determined that sounds that suggested chewing (33.4% of audio; see supplementary materials 7.3.6 for example clips), hopping (24.5%), silence (23.6%), and unclassifiable noises (9.3%) could be repeatedly distinguished and were the most common. Although we could not truly validate our sound classification for each behavior, we verified that these sounds could be repeatedly associated with a specific behavior among different observers. Three independent listeners blindly classified a subset of clips into the four categories, and we calculated inter-listener agreement for each type of sound.

We manually extracted 300 seconds of each sound associated with chewing, hopping, and silence consisting of 20-30 independent clips from each hare. Using 70% of the clips, spectrogram analysis (window=8000, overlap=50) was run on each second using the seewave package in R to determine the acoustic properties (Sueur et al., 2008). A classification algorithm consisting of upper and lower amplitude threshold values at 8 frequencies between 0 and 8 kHz for each sound (chewing, hopping, and silence) was created for each device. Thresholds were the 100% confidence intervals plus or minus 10% for that sound (Tables S7.3.4, S7.3.5 supplementary materials 7.3.3). However, if thresholds of two sounds overlapped at all frequencies, an optimization was run at the frequency where amplitudes were most distinguishable between sounds, and thresholds were adjusted to the value that generated the lowest misclassification. Any sound that did not meet all specified thresholds for chewing, hopping, or silence was classified as “other”. The accuracy of classification, unique to each recorder, was calculated using the remaining 30% of clips.

All audio files were converted to behavioral categories at a one-second resolution and used to tabulate an acoustic-based behavioral composition of the not moving and foraging categories from accelerometer classification for each hare, and across all hares. To account for drift in the internal clocks of the devices, prior to analysis we aligned the timing between devices by identifying 30 events across the file when both acceleration and acoustic amplitude shifted from a long bout of low values to a long bout of high values (i.e. resting to moving). A linear regression of time divergence over time of recording was calculated and the coefficients were used to readjust acoustic time. However, a ~20 second error remained post-alignment so behavioral composition was calculated using not moving and foraging accelerometer bouts longer than 90 seconds, with the first and last 30 seconds removed.

Daily time budgets and behavioral responses to moonlight

From both accelerometer-classified, and acoustic-classified behavior, we determined the daily time budgets of free-ranging individuals. This was calculated as the proportion of 24 hours that all hares spent expressing each behavior.

Moonlight illumination levels and daily light phase times (including moon rise and moon set times) for our study site were retrieved with *suncalc* package in R (Agafonkin & Thieurmel, 2017). Moonlight illumination levels were converted into a 3-level categorical variable according to the fraction of the moon that was lit: <0.33 (new), 0.33-0.66, and >0.66 (full). Eight light phases defined by the position of the sun relative to the horizon were used including: day (above horizon minus the first and last hour sunlight; ~4 hours), evening (last hour above horizon; ~1 hour), dusk (0 - 6° below horizon; ~1 hour), evening twilight (6 – 18° below horizon; ~2 hours), night (>18° below horizon; ~12 hours), morning twilight (18 – 6° below horizon; ~2 hours), dawn (6 - 0° below horizon; ~1 hours), and morning (first hour above horizon; ~1 hours). We removed all times when there was potentially cloud cover using both snowfall measures, which were collected daily from 4 locations throughout the study area, and hourly relative humidity values from the nearest weather station (Haines Junction, 40km away; Environment Canada). We removed all nights preceding a snowfall measurement greater than 0, and all times when the relative humidity was greater than 85%, since cloud cover is highly correlated with relative humidity (Sandor et al., 2000). Although we did not measure moonlight illumination levels ourselves and do not know the exact values that occurred, moon phase and lunar position are commonly used in studies of the effects of moonlight on wildlife (e.g., Johnson & De León, 2015; Gigliotti & Diefenbach, 2018).

As foraging and not moving were highly correlated (Pearson's correlation coefficient =-0.99), moonlight analysis focused on foraging with the understanding that any major changes seen in foraging times are mirrored by opposite changes in not moving. We quantified accelerometer derived hare behavior in response to moonlight at three temporal scales. At a daily scale, we examined foraging time per 24 hours using a generalized linear mixed effects model (GLMM) with moon phase (three level) as a fixed effect (R:lmer; Bates et al., 2015). At a within-day scale, we examined how foraging time (min/hr) was influenced by moon phase during different times of day using a GLMM with a light phase and moon phase interaction. At this scale we also tested how hopping (min/hr) and sprinting (events/hr) were influenced by moonlight across light phases. Hopping was examined using the same GLMM as foraging. Sprinting event data was zero-inflated so a hurdle model (Martin et al., 2005; Zuur et al., 2009) was used consisting of a binomial (logit-link) GLMM to test whether individuals sprinted or not during each light phase, and a second GLMM to test whether differences occurred in the number of sprint events during times when hares sprinted at least once. As behavioral states were analyzed separately, a Bonferroni correction (alpha=0.02) was applied to all analyses at this temporal scale. At an hourly scale, we examined how foraging time (min/hr) was influenced by the presence of moon using a GLMM with a moon phase and moon position (set or risen) interaction. This analysis only used hourly foraging values during the darkest light phase (night). All hours when the moon rose, or set were removed to reduce landscape-imposed variation in timing of rising and setting.

We included the intermediate moonlight levels in this analysis as it is during this part of each month that the moon rises or sets halfway through the night and the response to moon position relative to the horizon might be most pronounced. All GLMMs included hare ID as a random factor, and for the within-day and hourly scale analysis, date was included as a random factor. Model fit was calculated using conditional R-squared values, and significance of fixed effects were assessed using Wald chi-square (χ2) tests (Bolker et al., 2009).

Results

Accelerometer classification

We found that a ΔOA threshold value of 1.15 g-forces distinguished moving from not moving with a 95.8% accuracy using a sample window duration of 12 seconds. Not moving was correctly classified 94.6% (159/168 events) of the time, while moving had an accuracy of 97.0% (163/168 events; Figure 3.3). A ΔOA threshold of 3.0 g-forces over four seconds further separated any segment classified as moving into foraging (feeding, and short travel) and travelling with an accuracy of 88.1% (travelling = 83.1%, 242/291 events; foraging = 93.1%, 271/291 events; Figure 3.3). Finally, travelling-classified segments were divided into sprinting and hopping (low speed travel) using a OA threshold value of 6.5 g-forces over 4 seconds with an accuracy of 88.4% (sprinting = 76.9%, 10/13 events; hopping = 100%, 13/13 events; Figure 3.3). The overall accuracy of the classification into three behavioral states (not moving, foraging, and travelling), which accounts for all misclassifications at each level of the tree was 88.0% with slightly lower divisional accuracy than what was calculated when setting the threshold values (Table 3.1). Accuracy varied at the individual level from 80% to 91.7%, with large variation in individual accuracy of classifying travelling and foraging (see supplementary materials for

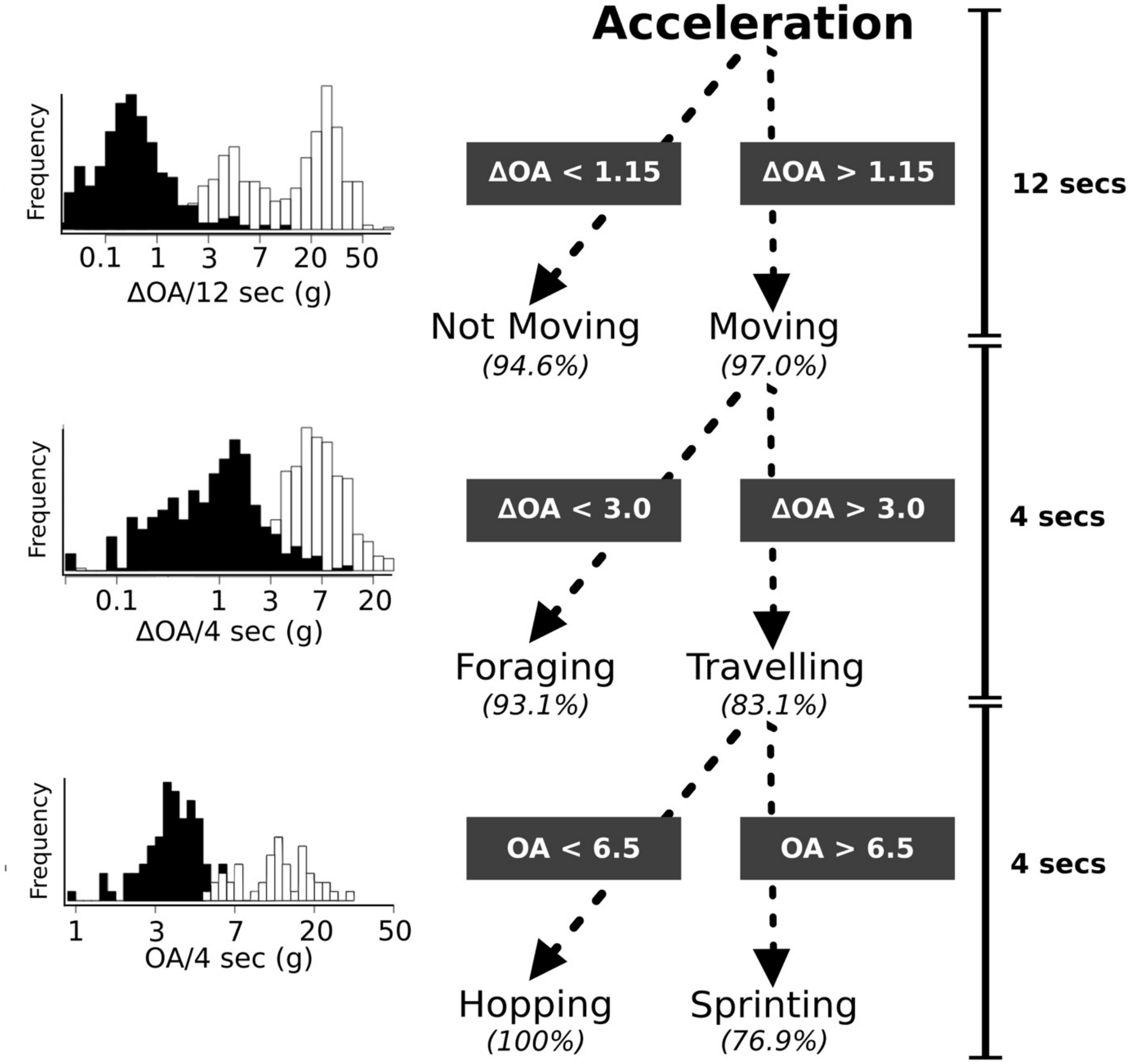

Figure 3.3 Hierarchal decision tree used to classify snowshoe hare accelerometer data to four behavioral categories. Long duration behavioral states were classified using a 12 second window, while short duration behavior was classified using a four second window. The accuracy of each division is the percentage of observed behavior that were classified correctly. Histograms depict the frequency of each behavior occurring at different values of the summary statistic used for the division of the tree. Black represents behavior on left side of the decision tree while white is behavior on right side of decision tree at each split.

individual confusion matrices 7.3.4). Classification using a random forest algorithm generated accuracies ranging from 83.3% to 96.7% depending on the sample window chosen (see supplemental materials Figure S7.3.2).

Table 3.1 - Confusion matrix of accelerometer-based classification of snowshoe hare behavior to three categories: not moving, forage, and travel. Overall accuracy is 88.0%

	Not Moving	Forage	Travel	Accuracy
Not Moving	68	7	0	90.7%
Forage	6	66	3	88.0%
Travel	0	11	64	85.3%

Refinement of accelerometer behavior categories using acoustic recorders

Three audio sounds (silence, chewing and hopping) could consistently be identified by listeners (see supplementary materials 7.3.6 for example clips; Table S7.3.3). Inter-rater reliability was 97% and 95% for chewing and silence, respectively. There was 83.3% agreement among all raters for “unclassifiable sounds”; some sound clips were suggested to be hopping or chewing, but there was no consensus across all listeners. Hopping had the lowest among-listener agreement (55.6%) with the most common alternative classification being unclassifiable sound. We are confident in our identification of these four sounds due to 1) the high inter-rater reliability scores, and 2) sounds labelled chewing, hopping, and silence primarily occurred when the hare was foraging, travelling, and not moving according to the accelerometer respectively. That being said, we have no means to truly validate that these sounds are the behavioral states classified. As such, our acoustic results should be taken with caution as there is a potential for misclassification.

Acoustic spectral analysis of user-classified sounds indicated that silence had no peaks in amplitude at any frequency, chewing had a peak at 250-600 Hz, and hopping had a primary peak at 0-650 Hz and secondary peak at 3650-4000 Hz (Figure 3.4), but peak frequencies varied between recorders (supplementary materials 7.3.3, Figure S7.3.3). Automated classification of these three acoustic behavioral states produced an accuracy of 94.1% (Table 3.2) with little variance in accuracy between devices (supplementary materials 7.3.5). Only 5.7% of acoustic files did not match the properties of these three behaviors and were classified as other sounds. The majority (~60%) of these other sounds were short in duration (1 second) and may have consisted of branches or parts of the hare hitting the microphone, or the hare shifting in position. In comparison, only a small amount of the silence (4%), chewing (9.4%) and hopping (22.8%) were short duration (1 second).

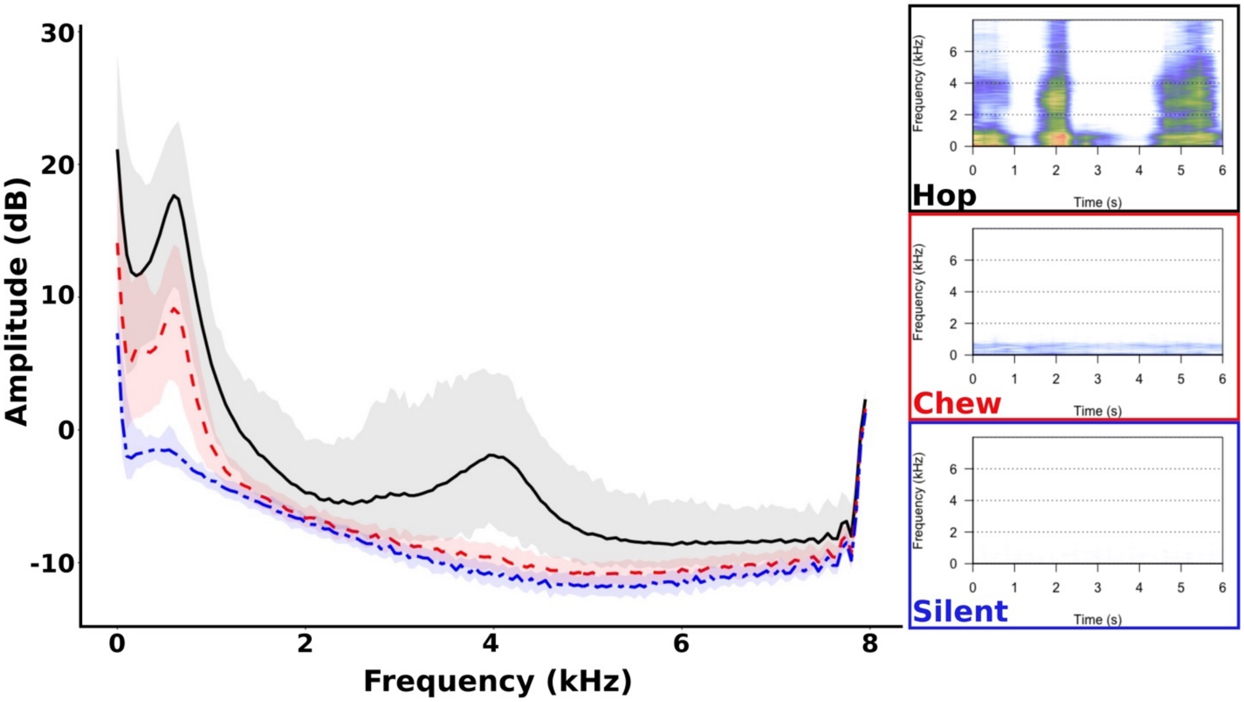

Figure 3.4 Amplitude frequency spectral properties of hop, chew and silent sounds from animal-borne acoustic recorders on snowshoe hares (right) and accompanying spectrograms (left). Shading represents the 95% CI of the amplitude for each behavior.

Table 3.2 - Confusion matrix of acoustic-based behavioral classification of snowshoe hare behavior to three categories: silence, chew, and hop. Overall accuracy is 94.1%

	Silence	Chew	Hop	Other	Accuracy
Silence	87	3	0	0	96.7%
Chew	0	84	2	4	93.3%
Hop	0	5	83	2	92.2%

Acoustic refinement of accelerometer classification revealed that bouts of foraging were composed of a combination of chewing (42.5%), hopping (35.7%), silence (13.0%) and other sounds (8.8%). The composition of foraging bouts varied among individuals (Figure 3.5a) but, on average, was consistent throughout the day (Figure 3.6). The behavioral composition of not moving was consistent among individuals and was composed of silence (~80%) chewing (~13%), other sounds (~4%), and hopping (0.3%) (Figure 3.5b). The composition of not moving varied with time of day switching from primarily silence during the day to primarily chewing at night (Figure 3.6).

Daily activity

We calculated average daily time budgets of free-ranging snowshoe hares in winter using accelerometer data from all individuals. Hares spent almost all of their time either foraging (~49%) or not moving (~49%) with small amounts of travelling (2%; i.e., either long duration hopping or sprinting). Not moving was the predominant behavior during daylight hours, and time spent foraging increased at dusk, remained high throughout the night, and decreased at dawn (Figure 3.6, 3.7a). Acoustic recorders revealed that snowshoe hares split their time between silence (46.3%), chewing (37.5%), and hopping (10.8%) with small amounts of other sounds

(5.4%). Hares were mainly silent during daylight, while at night they were chewing and hopping (Figure 3.6).

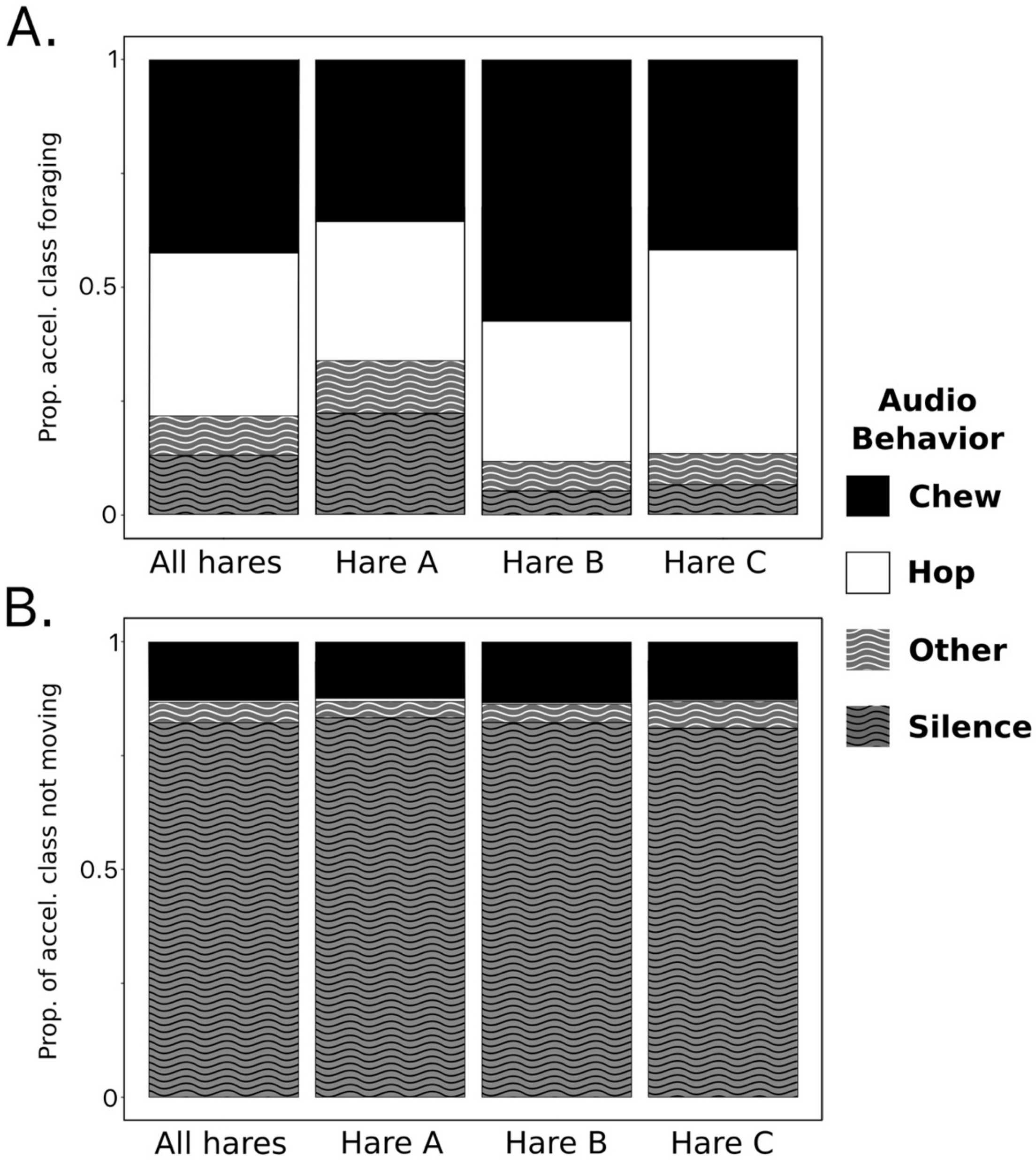

Figure 3.5 Acoustic determination of time spent chewing (black), hopping (white), silent (black stripe), and other (white stripe) during accelerometer-defined bouts of foraging (A) and not moving (B), across all individuals (n=3) and for each individual free-ranging snowshoe hare.

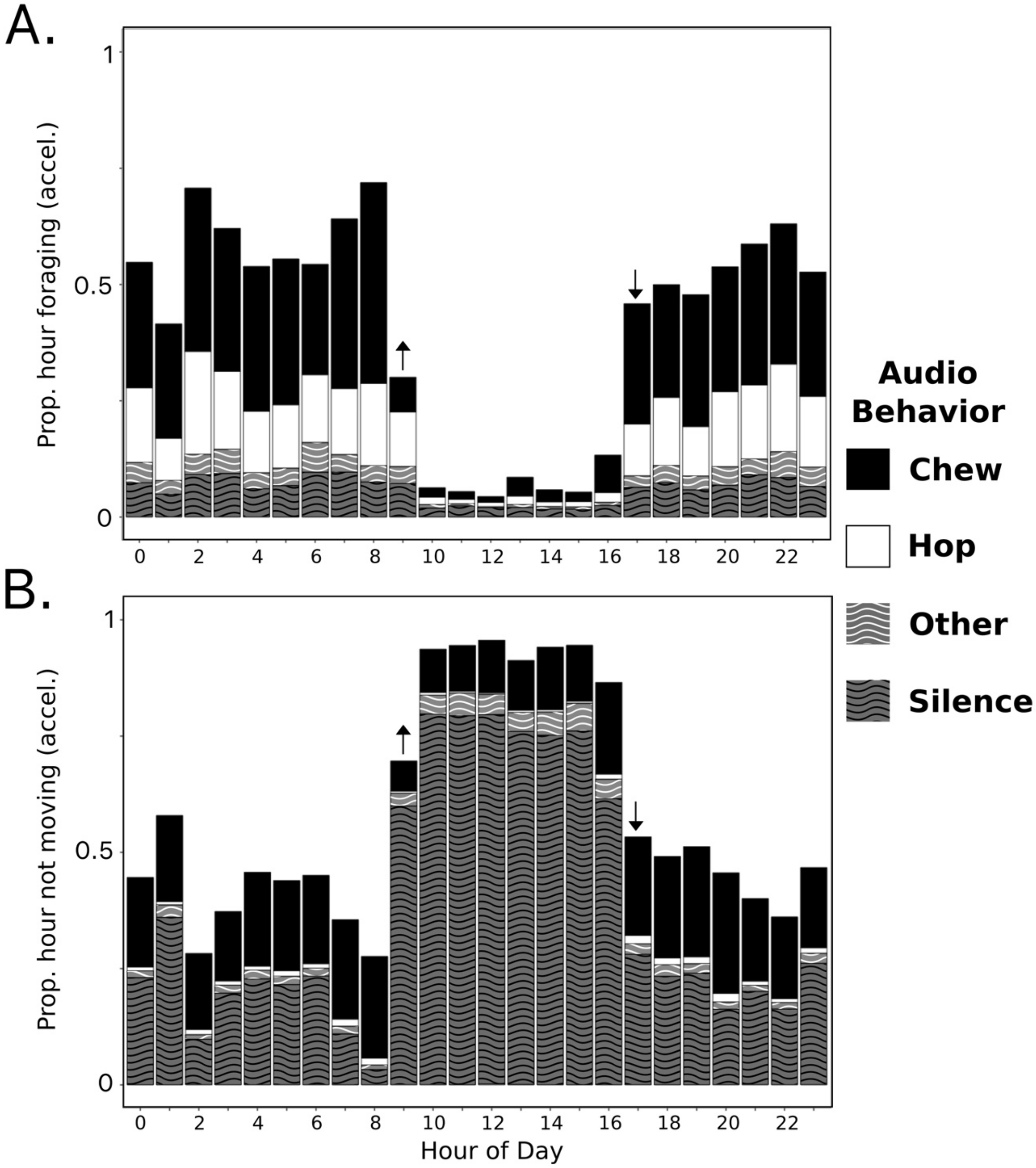

Figure 3.4 Accelerometer classification of the proportion of each hour of the day spent foraging (A) and not moving (B) and the acoustic composition (chewing: black, hopping: white, silence: black stripe, or other: white stripe) of those behavioral states. All data was collected over the same two days from free-ranging snowshoe hares (n=3) that were outfitted with an accelerometer and an acoustic recorder. Arrows denote sunrise and sunset times.

Moonlight analysis

Snowshoe hares decreased daily time spent foraging by 40 min per day during a full moon compared to during a new moon (χ^2=11.6, df=2, P=0.003, model $R^2_{(c)}$=0.23). Time spent foraging, hopping, and the occurrence of sprinting events during each light phase was influenced by the phase of the moon (foraging: χ^2=230.8, df=14, P<0.001, model $R^2_{(c)}$=0.69; hopping: χ^2=104.5, df=14, P<0.001, model $R^2_{(c)}$=0.37; sprinting: χ^2=42.9, df=14, P<0.001, model $R^2_{(c)}$=0.67; Figure 3.7), but the number of sprint events in a light phase was not influenced by the moon (χ^2=15.2, df=14, P=0.36, model $R^2_{(c)}$=0.32). Hares had the largest decrease in foraging time during the night, with an average decrease of 3 min/hr or 51 min between dusk until dawn during full moons compared to new moons (Figure 3.7b). Hopping, but not sprinting, was also substantially reduced through the darkest phases from twilight until dawn (Figure 3.7c, d). However, this pattern switched during dawn and morning following a full moon when hares spent noticeably more time foraging and hopping and were more likely to sprint than after a new moon (Figure 3.7b, c, d). Within a single night, snowshoe hare responses to the moon being above or below the horizon depended on the phase of the moon (χ^2=15.1, df=2, P<0.001, model $R^2_{(c)}$=0.30; Figure 3.8). When the moon was at its brightest (>0.66 fraction is visible), snowshoe hares spent more time foraging per hour during the hours that the moon was below the horizon than when the moon had risen (t= 2.07, df=1443, P=0.039; Figure 3.8). However, during all other phases of the moon (visible fraction is <0.66), hares decreased time spent foraging when the moon was below the horizon as compared to when it was above the horizon (fraction<0.33: t= -2.25, df=1436, P=0.024; fraction>0.33: t= -3.62, df=1444, P<0.001; Figure 3.8).

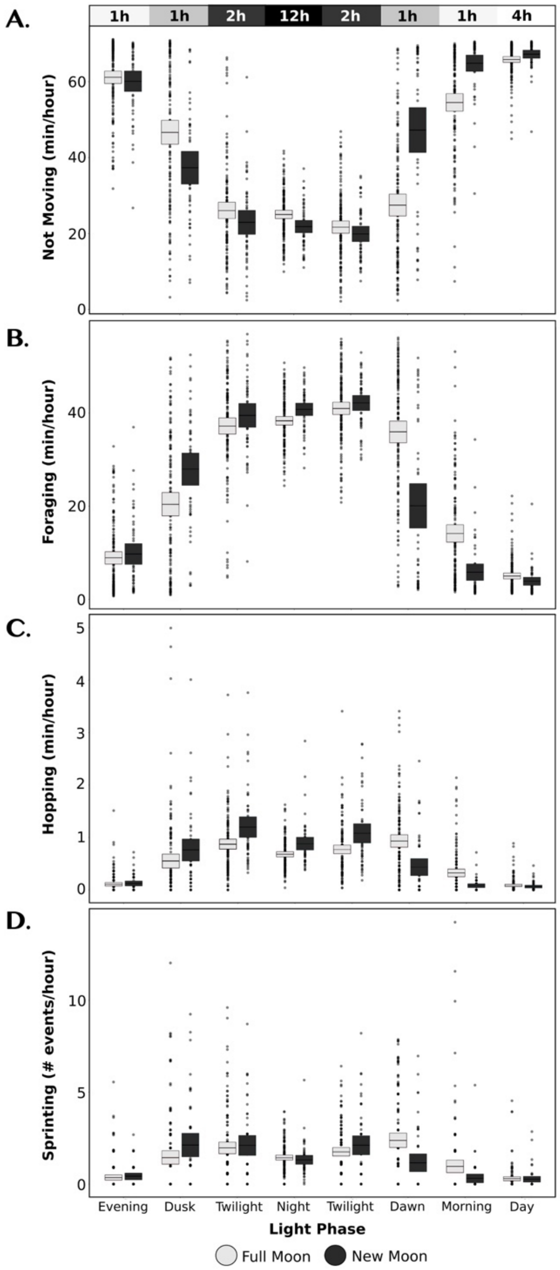

Figure 3.5 Average time spent by snowshoe hares on each behavior during different light phases of a day and moon phase with light boxes for full moon (lunar illumination > 0.66) and dark boxes for new moon (lunar illumination < 0.33) conditions (mean ± 95% CI). Not moving (A), foraging (B), and hopping (C) are presented as time spent (min/hr) expressing each behavior, while sprinting (D) is depicted as number of events per hour. Bar at top indicates the solar illumination level of each light phase and average number of hours that occur during that phase in a 24-hour period.

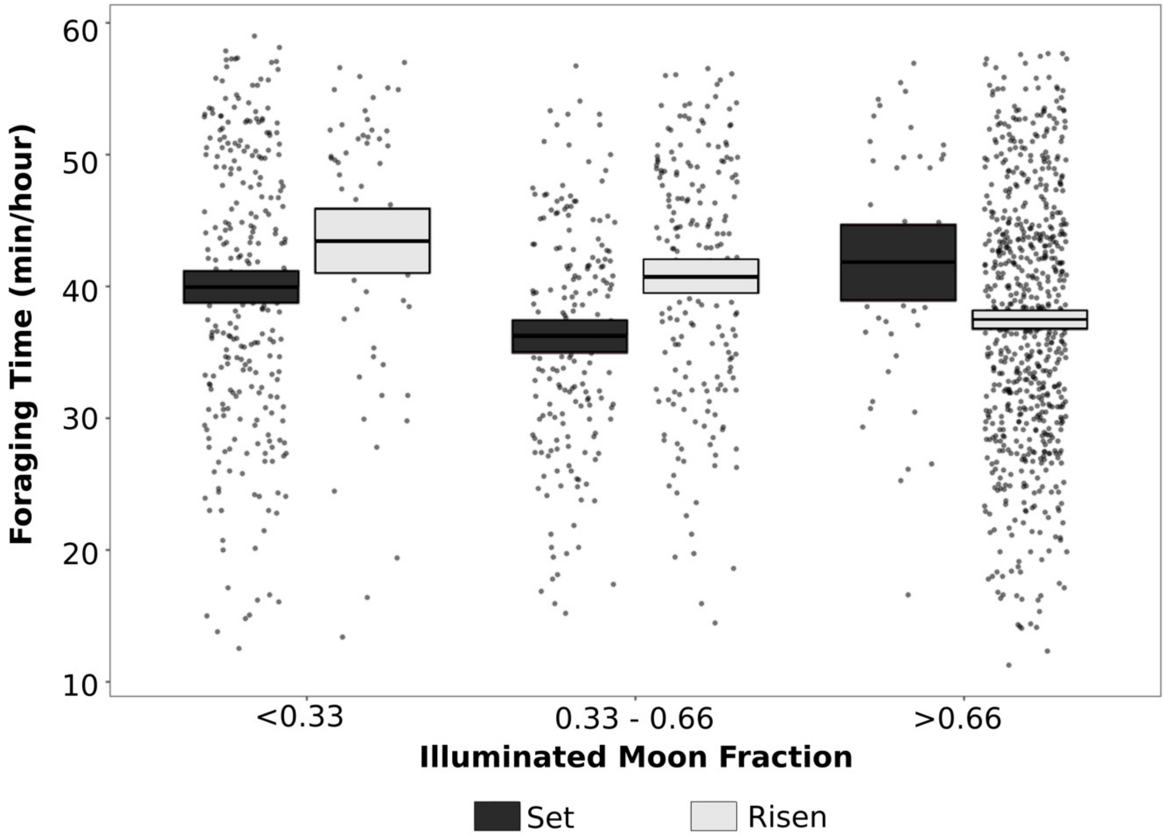

Figure 3.6. Average foraging time (min/hour) of snowshoe hares when moon is above (risen; light grey) or below (set; black) the horizon during different moon illumination fractions (mean ± 95% CI).

Discussion

By integrating two biologging technologies (accelerometers and acoustic recorders), we demonstrate the possibility of accurately classifying behavior of a nocturnal, and often difficult to observe, free-ranging mammal over multi-month durations. After achieving high overall accuracy for both accelerometer- and acoustic-based behavioral classification, we were able to explore the composition of broad accelerometer categories revealing inter- and intra-individual differences in behavior. Our demonstration of the potential for accelerometers to assess behavioral responses of hares to moonlight revealed that hares adjust their time spent foraging as light conditions change.

Biologging behavior

Despite general difficulties in observing cryptic species, we successfully recorded behavior of a nocturnal species for up to three months continuously using biologging technology. We found that different technologies were best suited for extracting specific behavioral states and that a combination of technologies may be necessary to understand the complex nature of a species' behavior. For example, although accelerometers could classify foraging behavior, the act of chewing in snowshoe hares did not generate a measurable amount of acceleration. In this particular study, our capacity to detect chewing was limited by low sampling regime but it is also likely that some behavioral acts, like chewing, may be difficult to detect using acceleration at any sampling frequency without adjusting the attachment of the device to a different location (such as to the jaw; Iwata et al., 2012). However, chewing was a behavior that was easily identifiable on the acoustic recorders. Travelling, on the other hand, was more accurately distinguishable with accelerometers than through acoustics. Additionally, while we were significantly below the Nyquist criterion for a hare hop (Brown et al., 2013), we show that accurate classification is possible to accuracies (88.0%) comparable to those achieved (75% to 98%) using higher frequencies (3.3 Hz to 40 Hz; Nathan et al., 2012; Bidder et al., 2014; McClune et al., 2014; Hammond et al., 2016). At this lower frequency, the detail of behavioral categories (e.g., foraging instead of feeding and individual hops) is compromised to maintain accuracy. This compromise will not suit researchers interested in describing steps or wingbeats over the span of days, but for researchers interested in behavioral changes over the span of months this will likely be a negligible cost.

Our use of animal-borne acoustic recorders not only provided a means of determining behavioral composition of accelerometer classification, but also demonstrated an alternative technique for collecting continuous behavioral data in circumstances when other methodologies might not be possible. Despite only recording on a few individuals (n=3) for a short duration to test the potential of this technology, we revealed that individual and temporal variation exists in the composition of accelerometer-classified foraging and not moving categories. Although sounds like chewing were easily identifiable, other sounds could not be identified to a particular behavior with any confidence. For this reason, validating acoustic data with behavioral observations would be recommended in order to generate a more detailed classification than what we presented here. Acoustic recorders are rarely used for non-vocal behavior despite their commonality in animal communication research (e.g., Bee & Gerhardt, 2001; Reby & McComb, 2003; Fischer et al., 2004). However, successful applications of acoustics to record behavior all highlight the considerable wealth of information contained in this media form including bodily functions (e.g., heart rate; Couchoux et al., 2015), behavior (e.g., chewing, grooming, wingbeats; Ilany et al., 2013; Stowell et al., 2017; Wijers et al., 2018), and environmental noise (e.g., anthropogenic noise, wind, vocalization of other species; Lynch et al., 2015; Stowell et al., 2017).

Daily activity

Analyses of both accelerometer and acoustic information revealed that snowshoe hares split their time primarily between not moving and foraging-related behavior with limited time spent travelling. This is a similar pattern as seen in other hare species where vigilance, rest and feeding represented over 95% of the day (Lush et al., 2016). At least in winter, when nights are long and dark, we found that snowshoe hares are characterized by a single daily activity peak centered in the night, with elevated activity extending into dawn and dusk. The limited literature on the behavior of free-ranging snowshoe hares generally classifies the species as exhibiting either crepuscular (Murray, 2003) or nocturnal (Foresman & Pearson, 1999) activity patterns. Using the definition of Anderson & Wiens (2017) and Bartness and Albers (2000), snowshoe hares are likely best classified as a nocturnal species, but alternatively as a nocturnal species with activity that extends into the crepuscular period.

Response to moonlight

For nocturnal animals, moonlight can drastically change the landscape, and impacts the tradeoff between foraging and predation risk (Prugh & Golden, 2014; Gigliotti & Diefenbach, 2018). We found that moonlight conditions caused snowshoe hares to make substantial adjustments in behavior throughout the night, with the magnitude and direction being dependent on the light phase. During the darkest phases of the night (dusk to morning twilight), travelling was reduced by ~30% and foraging by ~6% when the moon was full. This reduction in foraging is considerably less than the average reduction found in foraging trials (13.6%) across all species where it has been tested (Prugh & Golden, 2014), but the disproportionate reduction in travelling to foraging suggests that the snowshoe hares were not moving around their environment in the same manner while foraging. These responses to moonlight confirm previous studies in snowshoe hares that have reported decreased activity and adjustments in habitat use under full moon conditions (Gilbert & Boutin, 1991; Griffin et al., 2005; Gigliotti & Diefenbach, 2018). Although we could not directly measure whether moonlight impacts predation risk, increased illumination at night has been linked to increased activity and feeding in various predators including coyotes (Kenaga et al., 2013) and *Lynx* spp. (Rockhill et al., 2013; Heurich et al., 2014). The reduction in activity under full moons suggests that snowshoe hares change their behavior to reduce risk of predation.

Hares appeared to behaviorally compensate for the lost foraging time associated with full moons via an extension of foraging into morning daylight hours. Such compensatory temporal shifts in behavior due to moonlight have also been shown to occur in other species (e.g., *Dipodomys merriami*; Daly et al., 1992). All animals have minimum energy intake requirements that must be achieved through daily foraging (Norberg, 1977) and although some species can reduce this requirement (e.g. through fat storage or use of torpor), snowshoe hares who have limited body fat stores (~ 4 days resting metabolic support; Whittaker & Thomas, 1983) must forage on a daily basis. This nutritional constraint seems to translate to drastic adjustments in temporally-explicit foraging choices rather than changes in overall foraging time as light conditions change (Gilbert & Boutin, 1991). If choice in timing of foraging is directly related to predation risk, then in hares, moonlight shifts risk of predation from relatively low to relatively high during the night to the extent that it is perceived to be safer to forage in the morning than maintain high foraging rates during the night.

A second compensation that seems to occur is that adjustments in behavior made during the night counteract any increases in predation risk that would be expected. We considered sprinting to be a measure of flightiness, as although some sprints occur from direct predator encounters, the majority are likely responses stemming from wary behavior (Vasquez et al., 2002). If the amount of flightiness is related to the amount of perceived predation risk, as would be expected, then the lack of effect of moonlight on sprinting during the night (Figure 3.5d) suggests that hares reduce their time spent foraging to minimize the level of predation risk, creating a constant level of risk across moonlight conditions. However, the increased sprinting during dawn and morning periods following full moon nights suggests the morning compensational foraging bouts come at a cost. This increased level of perceived predation risk may be due to the morning period being a time when all predators can be active. Predators of hares are characterized as nocturnal/crepuscular (*Lynx canadensis, Canis latrans, Bubo virginianus*), or diurnal/crepuscular *(Accipiter gentilis)*, but many nocturnal species have considerable movement into and throughout the day, especially in winter, making the morning a time when both primarily nocturnal and diurnal predators may be hunting (Ozoga & Harger, 1966; Squires & Reynolds, 1997; Kolbe & Squires, 2007; Arias-Del Razo et al., 2011; Artuso et al., 2013). Despite this increased risk during the compensatory foraging, the strategy of reducing foraging during the night likely results in lower exposure to risk overall.

We additionally found that the extent of moonlight avoidance by snowshoe hares was dependent on the phase of the moon, with diminished foraging times when the moon was above the horizon on full moon nights and below the horizon on partial or new moon nights; a switching of preference that has not been observed previously. Generally in other species, individuals are found to be more active during the darkest hours when the moon is below the horizon regardless of moon phase (Morrison, 1978; Daly et al., 1992). This switching of preference for moonlight would suggest that risk is highest when light conditions are either at their brightest or darkest (Prugh & Golden, 2014). The main predators of snowshoe hares all rely on visual cues for hunting (Wells, 1978; Artuso et al., 2013). As such, a decrease in activity with increasing light may be a response to higher hunting efficiency from their predators through improved vision. Although the darkest conditions may inhibit the predators ability to hunt (Wells, 1978), these conditions will have similar effects on the hares ability to detect predators as they also rely partially on visual senses to detect danger. It may be that the loss of use of one of their senses is enough to cause the hares to select against these conditions for foraging, even if predators are similarly hindered.

Biologgers provide us with the opportunity to investigate detailed behavioral adjustments over long temporal timeframes revealing subtle and short-term responses to environmental change. Every biologging technique has strengths and weaknesses, however, combining biologging technology in complementary ways can allow a circumvention of such issues. Short duration acoustic recorders provided a method of collecting behavioral states of a free ranging nocturnal animal that were not possible with accelerometers and vice versa. This allowed for easier interpretation of the behavioral classification generated from long duration accelerometers. Such multi-faceted approaches will allow us to gain the most detailed insight yet into behavioral responses of species to environmental change.

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Linking Statement

In the previous two chapters, I explored different biologging technologies and developed species-specific decision trees for classifying acceleration into behaviour for red squirrels and snowshoe hares. In both chapters, applications of this classification to data from free-ranging individuals indicated that individuals adjust their behaviour to changing conditions. The next chapter builds on these early indications of behavioural flexibility to explore how environmental variability drives activity patterns in endotherms. Combining accelerometer data collected over four years on red squirrels with measures of resource availability, mating opportunities and temperature, I examine how squirrels respond to seasonal and multiannual fluctuations in their environment and use that to build a bioenergetic behavioural decision model to predict activity across seasons and years.

Chapter 4 - Optimization of energetic and reproductive gains explains behavioural responses to environmental variation across seasons and years

Abstract

Animals switch between inactive and active states, simultaneously impacting their energy intake, energy expenditure and predation risk, and collectively defining how they engage with environmental variation and trophic interactions. We assess daily activity responses to long-term variation in temperature, resources, and mating opportunities to examine whether individuals choose to be active or inactive according to an optimization of the relative energetic and reproductive gains each state offers. We show that this simplified behavioural decision approach predicts most activity variation (R2=0.83) expressed by free-ranging red squirrels over four years, as quantified through accelerometer recordings (489 deployments; 5066 squirrel-days). Recognizing activity as a determinant of energetic status, the predictability of activity variation aggregated at a daily scale, and the clear signal that behaviour is environmentally-forced through optimization of gain, provides an integrated approach to examine behavioural variation as an intermediary between environmental variation and energetic, life-history, and ecological outcomes.

Introduction

Behaviour can be defined as choices made by whole organisms, which have purpose and take time (Baum, 2013; see also Levitis et al., 2009). In many cases, animals choose where to be and what to do with the purpose of increasing access to resources while reducing the risk of predation (Lima & Dill, 1990; Brown, 1992; Werner & Anholt, 1993; Brown et al., 1999). Given behavioural decisions relate directly to food, predators, and reproduction, how behaviour varies over time links environmental variation to rates of consumption and predation, reproduction and survival, and ultimately population dynamics and trophic interactions.

However, successful documentation of behavioural responses to environmental variation and their ecological consequences has been limited by at least three major impediments. Methodologically, the difficulty of quantifying animal behaviour outside of the direct presence of a human observer has often constrained behavioural research to temporal extents and observation windows that are much shorter than, and not fully representative of, seasonal and multi-annual environmental variation (Altmann & Altmann, 2006). Empirically, behavioural variation is multi-dimensional, including but not limited to movement, feeding, and social behaviour (Martin & Bateson, 1993), making it challenging to characterize behavioural responses in a generalized, yet ecologically-relevant manner. Finally, conceptually, the importance of behaviour in defining the energetic and ecological status of animals has often been misrepresented or neglected in physiological models and ecological theory. For example, the metabolic theory of ecology has focused primarily on body size and temperature - but not behaviour - as determinants of metabolic variation (Brown et al., 2004; Humphries & McCann, 2014). Meanwhile, consumer resource theory allows for behaviour to affect the consumption of resources, but treats energy expenditure as behaviourally-independent (Yodzis & Innes, 1992; Post et al., 2000). The methodological constraint requiring direct observation of behaviour has now largely been eliminated by recent advances in biologging technologies which offer effective methods for continually recording fine-scale behavioural variation (Kays et al., 2015) over long durations (Williams et al., 2016; Tatler et al., 2018; Studd et al., 2019). Accordingly, we focus the next two paragraphs on describing an empirical approach for categorizing behavioural variation and a conceptual approach to relating these behavioural categories to their energetic and ecological consequences.

A simple way to classify behaviour in an ecologically and energetically-relevant way is to consider inactivity and activity as contrasting states. Inactivity (stationary, not feeding, and within a refuge) minimizes energy losses and predation risk, whereas activity (moving, feeding, and outside of a refuge) is necessary for energy acquisition and mating (Daly, 1978; Werner & Anholt, 1993; Luttbeg et al., 2003). Of course, the specificities and correlates of particular active and inactive states vary widely both among animals and within the same individual over time. Nevertheless, because all animals punctuate active bouts with periods of inactivity, these two states capture behavioural variation in a generalizable way where activity is focused on acquisition and expenditure whereas inactivity is focused on conservation and recuperation.

Animals can be thought of as energy processors that acquire energy from the environment and allocate this energy among maintenance, growth, and reproduction (Yodzis & Innes, 1992). Considering animals in this way situates energetic status as the mechanistic link connecting environmental variation, including that in resource availability and thermal conditions (Scholander et al., 1950; Mueller & Diamond, 2001), to the survival and reproduction of individuals, and the demographics of populations. In considering bioenergetic responses to environmental variation, energy expenditure is often measured and modeled as behaviourally-independent (Yodzis & Innes, 1992; Brown et al., 2004; Humphries & McCann, 2014). However, for all animals, acquiring resources requires activity, and activity requires energy expenditure (Kam & Degen, 1997; Humphries & Umbanhowar, 2007). Energetic surplus is achieved only when the energy gains offered by activity exceed its energetic cost. Behavioural activity is thus a fundamental, but under-appreciated, determinant of how environmental variation affects the energetic status of organisms. Although other areas of research in ecology and evolution consider behaviour-energetic linkages more explicitly, like the possible co-evolution of metabolic and behavioural traits (i.e. metabolism and personality traits; Careau et al., 2008; Biro & Stamps, 2010; Mathot & Dingemanse, 2015) or the link between locomotory performance and ancillary change in metabolic traits (Rezende et al., 2009; Careau et al., 2011), these areas of research tend not to focus on how shared variation in activity and energetic status drive ecological responses to environmental variation.

Here we extend energetically-explicit optimality models to predict activity responses of free-ranging organisms across seasonal and multi-annual variation in resources and temperature. Although considering behavioural decisions as optimizations has been central to foraging models (Pyke et al., 1977; Brown et al., 1999), this has generally, although not completely (e.g., McNamara & Houston, 1987), been restricted to understanding short-term decisions like prey and patch selection (Brown, 1992; Kramer, 2001). Since shifting the scale of focus often changes the nature of behavioural variation (Levin, 1992), it is important to assess whether the same optimality models traditionally applied across short-term conditions are able to predict activity across long time scales. Here, we hypothesized that behavioural responses to seasonal and multiannual variation in resources, temperature, and mating are optimized according to energetic and reproductive gain. This hypothesis, and the empirical comparisons and modelling approach described next, do not explicitly include temporal changes in predation risk as a driver of activity variation, a limitation which we revisit in the discussion. The current study measures the extent of daily, seasonal and annual variation expressed by 225 free-ranging North American red squirrels (*Tamiasciurus hudsonicus*) and explores how activity of non-lactating individuals varies across temperature (+/-50°C), day length, (+/- 17 hour), resource availability (20x change), and seasonal mating periods. We then develop an optimality model, based on the short-term energetic decision to be active or inactive according to prevailing environmental conditions to predict daily activity. By comparing measured and modeled activity across the full extent of environmental variation, we show that despite the perceived complexity of behaviour, seasonal and multiannual activity patterns are highly predictable from a remarkably few number of biotic and abiotic factors.

Materials and Methods

Measuring Activity in Relation to Temperature, Resources, and Mating Opportunities

We used accelerometers to measure activity on 225 individual red squirrels over three and a half years (2014-2017, deployments=489; squirrel-days=5066). This biologging research focuses on a bottom-up regulated population in the Kluane region of southwestern Yukon (61°N, 138°W) that has been the focus of long-term monitoring since 1987 (McAdam et al., 2007; Krebs et al., 2014). As a free-ranging study population, red squirrels offer several advantages in documenting drivers of activity variation, including year-round residency, large sample size, daily and seasonally variable activity patterns (Pauls, 1977; Studd et al., 2016; Studd, Landry-Cuerrier, et al., 2019), quantifiable resources (LaMontagne et al., 2005; Fisher et al., 2019), and most importantly, the ability to accurately classify activity and inactivity on undisturbed individuals using accelerometers (Studd, Landry-Cuerrier, et al., 2019).

Individual squirrels were captured on defended territories, weighed, assessed for reproductive condition, and fitted with an accelerometer (models Axy2/Axy3, 4 g [1.7% of body mass], Technosmart Europe) in collar form, either ventrally mounted on its own (n=128) or dorsally-mounted in combination with a ventrally-mounted VHF radio transmitter (n=361, model PD-2C, 4 g [1.7% of body mass], Holohil Systems Limited, Carp, ON, Canada; see Studd et al., 2019 for collar design). All accelerometers recorded acceleration between +/- 8 g_{forces} at a sampling rate of 1 Hz and temperature at a rate of 0.1 Hz, frequencies that have been shown to capture broad-scale behaviour of small animals with high accuracy, allowing for long-duration recordings (Tatler et al., 2018; Studd et al., 2019). Squirrels were released at site of capture and remained free-ranging until recaptured for collar removal (3 - 103 days later). Accelerometer data was processed and classified into two behavioural states, active (physically moving outside a nest) and inactive (physically not moving or inside a nest) using two thresholds described in detail in Studd et al (2019). Briefly, animals were in nest when the collar temperature was above the threshold value from a k-means clustering of all collar temperatures recorded that day (2 clusters), and were moving when the 10 second sum of the changes in acceleration from one second to the next was greater than 1.06 g_{forces}. We first assessed timing of activity by calculating proportion time spent active during 4 different light phases: day, dusk (sunset to start of civil twilight), night, and dawn (end of morning civil twilight to sunrise). Then, we calculated daily activity as the proportion of 24 hours in which squirrels were active. All procedures were approved by animal care committee at McGill University (Animal Use Protocol #4728) and were conducted under Yukon Territorial Government *Wildlife Research Permits* and *Scientist and Explorers Permits.*

Ambient temperature, T_a, was calculated at 15-minute intervals from recordings at nine locations across or near the study site. Our index of resource availability, R_a, reflects within and among year variation in the abundance and accessibility of key food sources to red squirrels and is based on quantified production, hoarding, and consumption of spruce cones, the primary food source for this population, in combination with direct feeding observations of alternative resources (n = 22,513). We distinguished each food source according to resource saturation characteristics (the extent to which additional resource gain diminishes as resource exploitation time increases) by categorizing between resources that were subject to intake saturation because they can only be consumed when encountered, and those that were alleviated from short-term saturation constraints because they can be hoarded for later consumption. This index of resource type, R_t, ranged from 0 when all available resources were only consumable (including previously hoarded items) and 1 when all available resources are hoardable. Finally, our mating opportunities variable was the product of the number of mating events each week by the probability of offspring recruitment as observed annually within the population. Details of how each explanatory variable was measured in the field, and subsequently calculated can be found in supplementary materials 1, 2, and 3.

Statistical Analysis

We tested when within the diel period squirrels were active, and whether that changed through the year using an ANOVA with an interaction between time of day (dawn, day, dusk, night) and season (spring, summer, autumn, winter). Season was defined according to normalized difference vegetation index values extracted for the study area from MODIS (winter: NDVI <

0.35, spring: 0.35 < NDVI < 0.61 and day of year < 200, summer: NDVI > 0.61, autumn: NDVI < 0.61 and day of year > 200; Didan, 2015). Following this analysis, we tested whether activity between sunrise and sunset (represented as proportion of 24 hours) was driven by R_a, R_t, T_a, mating opportunities, or a combination of these variables by building competing GLMM models for binomial data with a logit link. When testing models with combinations of variables, we included a three-way interaction (R_a, R_t, T_a) and a two-way interaction (R_a and mating). Since mating occurs when only non-hoardable resources are available, we split mating into two variables: a 2-level categorical variable (mating or non-breeding), and a continuous variable of mating opportunities which was only tested for values greater than zero when $R_t = 0$. All models included random effects of squirrel ID, and observation level (to control for over-dispersion; dispersion parameter ~1). Models were compared using AIC. Additionally, we tested the same variables in a generalized linear model (binomial) of daily mean activity values to determine the explanatory power of the model at explaining population level variation in activity over time.

Modelling Activity in Relation to Temperature, Resources, and Mating Opportunities

We constructed an energetic and mating optimization model to assess how, in theory, daily activity should respond to variation in temperature, resources, and mating opportunities if animals optimize inactive and active states. A basic version of this model is described in Humphries and Umbanhower (2007), elaborated here to incorporate additional documented drivers of red squirrel activity patterns, including diurnality (Pauls, 1977), food hoarding (Fletcher et al., 2010; Archibald et al., 2013), and access to thermal refuges (Humphries et al., 2005; Guillemette et al., 2009). Despite the red squirrel focus, the overall modeling should be generalizable to other animals that vary behaviour in response to bottom-up drivers, because it is based on commonalities of endotherm behaviour and energetics (highlighted below).

Optimal daily activity, expressed as the proportion of time that an animal is active in a day, is modelled as the sum of a series of decisions made throughout the day as to whether to be active or inactive at a given moment. We assume animals base this choice according to which state maximizes net energy gain (G_e) and net reproductive gain (G_r) such that:

$$Behaviour[\text{Active, Inactive}]\ (G_e,\ G_r,) = \begin{cases} Active & if\ G_{ea} > G_{ei}\ or\ G_r > 0 \\ Inactive & if\ G_{ei} \geq G_{ea}\ and\ G_r = 0 \end{cases} \qquad (1)$$

where G_{ea} is the net energy gain if active, G_{ei} is the net energy gain if inactive, and net energy gain is represented by:

$$G_e = I - E \qquad (2)$$

where I is the energy ingested and assimilated, and E is the energy expended (see Humphries & McCann, 2014). Given **acquiring resources requires activity**, it follows that G_{ei} is always characterized by $I = 0$, such that

$$G_{ei} = -E_i \qquad (3)$$

where E_i is the rate of expenditure when inactive. Given that **activity offers the possibility of intake at the expense of increased energy expenditure**, it follows that

$$G_{ea} = I - AE_{\mathrm{i}} \qquad (4)$$

where A is an activity multiplier equal to the factor that expenditure is increased above inactivity. Because **cold temperatures, below an endotherm's thermoneutral zone, increases energy expenditure**, it follows that

$$E = f(T_{\mathrm{a}}) \qquad (5)$$

where T_a is air temperature and the function, f, assumes a Scholander-Irving thermoregulatory response (Scholander et al., 1950). Given the potential that thermoregulatory costs can be **reduced by occupying a thermal refuge when inactive,** then

$E_a = f(T_a)$ (5a)

$E_i = f(T_a, Q)$ (5b)

where Q is refuge quality varying from 0 if the refuge offers no thermoregulatory benefit to 1 if it eliminates all costs of thermoregulation. Heat-generated by activity can substitute for the costs of thermoregulation, but this was not incorporated into the current model because substitution potential is eliminated when refuge quality (Q) is high and, even when Q is 0, substitution tends to be small or undetectable among small endotherms with a high surface to volume ratio (Humphries & Careau, 2011). With this model structure, energy expenditure varies according to activity, but also in relation to other factors including resting metabolic rate and thermoregulation. Because **intake can saturate over time**, we assume that I_t (I at time interval t) decreases relative to the previous time interval, t-1, according to:

$I_{(t)} = R/\alpha^{(t-1)}$ (6)

where R is resource abundance and α is a diminishing returns coefficient in which $\alpha = 1$ represents no diminishing returns, and $\alpha = 2$ represents a diminishing return of half the intake of the previous time period of foraging. The possibility that **resource types vary in their rate of saturation**, is accommodated in the model by allowing α to vary by resource type. The reality that **at particular times of the year, mating success requires activity unrelated to foraging gains** is added to the model by assuming reproductive gain, G_r,

$G_r = nqm$ (7)

where n is the number of potential mating events, q is the quality of offspring produced by mating, and m is a mating conversion factor equal to the rate at which activity is expected to increase per unit of nq. Finally, the tendency that **organisms express periodicity in activity patterns over a 24-hr cycle** is integrated into our model through a conditional argument restricting activity to the diel period (e.g. diurnal, nocturnal) within which the species is most active.

To explore optimal activity responses to a range of hypothetical temperature, resource, and mating opportunity conditions, we ran a series of simulations under two main frameworks. The first explored activity responses to the environmental conditions that influence G_e, by varying temperature, resource availability, and resource type. The second simulations explored activity responses generated by G_r by varying mating opportunities (qm) and resource availability. See supplementary materials 4 for elaborated versions of equations 1-7, and a table defining all variables, units, and parameter-values used in simulations (Table S1).

Comparing Measured and Modelled Activity Patterns

We tested the ability of our model to predict animal activity using measurements of squirrel resource availability, diet composition, mating events, juvenile recruitment, and air temperature for R_a, R_t, n, q, and T_a respectively. After generating a predicted value for daily activity for each day of the 3.5-year study duration, we assessed the correspondence of observed (measured) and predicted (modelled) activity by calculating the percentage of days where predicted activity was within 1.2 hours and 2.4 hours of the daily mean observed value (647 days with >3 squirrels). The parameters that were not directly measured or previously known were the mating conversion factor (*m*), the scaling of R_a, and the diminishing returns of the two resource types (hoardable and non-hoardable). We set *m* according to the empirically observed slope between activity and mating opportunities at average resource levels (R_a=30; $m = 0.016$). R_a was scaled proportionately so the lowest resource value generated enough active gain for at least 15 minutes of activity in a day at -20°C. Using measured activity, we assessed how varying the value of $\alpha_{\text{Hoardable}}$ and $\alpha_{\text{Non-hoardable}}$ influenced the accuracy of our model (see Supplemental Materials 4 for details).

Results

Measured Activity

Squirrels were primarily inactive at night and active during the day with some activity during dawn and dusk (Fig. 1), but the amount of activity was seasonally dependent (F=505, df=9, P<0.001; Fig. 1a-d). Squirrels were most active in autumn, averaging 75.2% of daylight hours (10.1 hours), and least active in winter, averaging 43.1% of daylight hours (3.73 hours). Activity during the night averaged 2% (9 min; range 0 – 70 min) with little variation between seasons. Dawn and dusk activity was generally limited (~ 5 min per period) except during autumn when activity would begin during the dawn period (~ 16 min per period).

Red squirrel activity varied seasonally and multi-annually, with individual values ranging from 1 hour to 15.5 hours per day (Fig. 2). The models with the most support (weight = 1) explained approximately 13% of the variation in activity at the individual level (conditional $R^2 = 0.13$; Table S2) and 88% of daily activity variation observed at the population level (adjusted $R^2 = 0.88$). Activity was dependent on interacting effects of resource availability, resource type, and

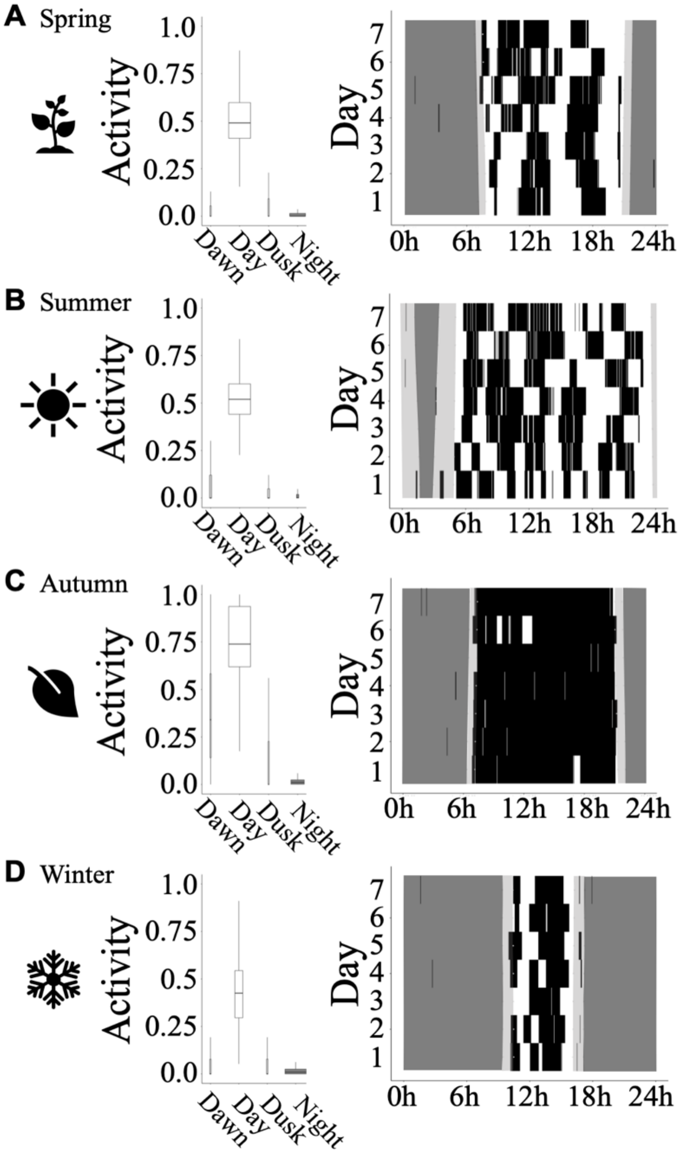

Figure 4.1. Seasonal variation in observed red squirrel (n=225) activity and inactivity throughout the day recorded using accelerometers. The timing and amount of activity varies according to each season (spring (A), summer (B), autumn (C), and winter (D)). Timing of daily activity is presented as proportion of photoperiod phase that squirrels were active (left), along with an actogram illustrating how activity (black) is organized within each time period (right). Each day is subdivided into four photoperiods in each figure: dawn (light grey shading in actogram), day (white), dusk (light grey) and night (dark grey) with the relative length of each phase represented by the width of box. Actograms display 7 days of activity and inactivity for a randomly selected individual.

air temperature (z = 356.8, $p < 0.001$). The lowest activity levels occurred when cold temperatures coincided with low availability of non-hoardable resources, and the highest activity levels occurred when warm temperature coincided with high availability of hoardable resources (Fig. 3a). Activity generally decreased as temperature decreased below 10°C, decreased or remained constant at temperatures above 10°C, increased with increasing resource availability, and increased as the proportion of hoardable resources increased (Fig. 3a). However, the strength of the activity response to these three environmental variables was inter-dependent. For example, when resources were non-hoardable (strongly saturating), increased resource availability reduced the effect of temperature on activity, and when resources were hoardable (weakly saturating), increased resource availability increased activity regardless of temperature (Fig. 3a). Activity response to mating opportunities was dependent on resource availability. Males during the

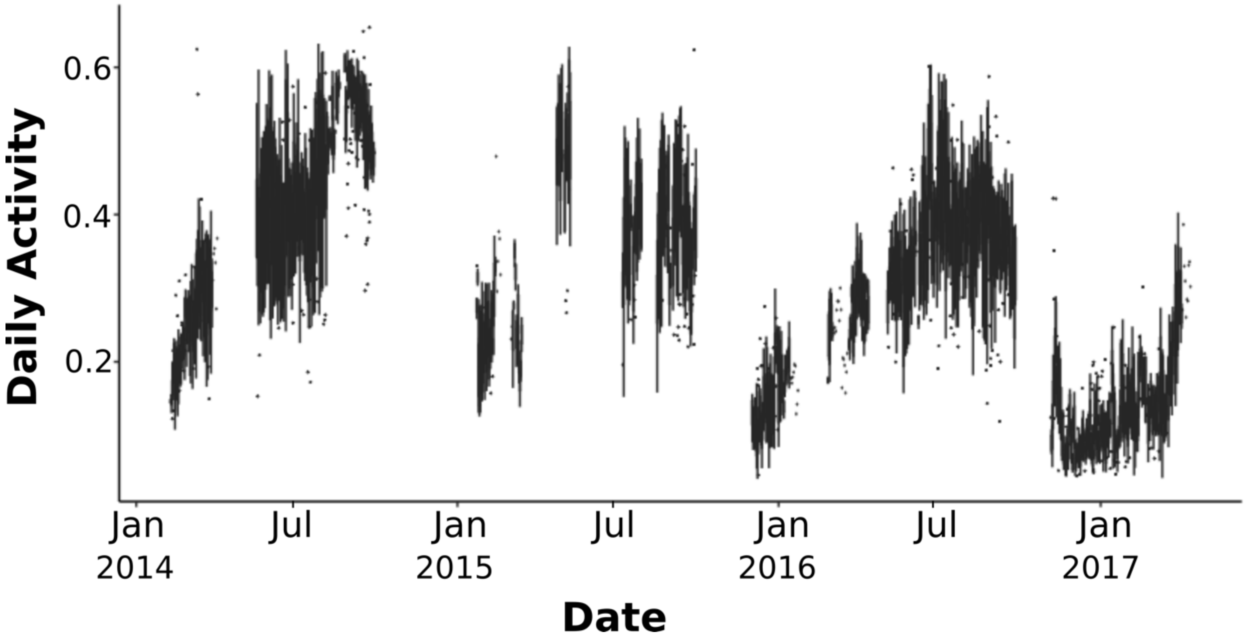

Figure 4.2. Observed daily activity (proportion of 24 hours) of free ranging red squirrels (n = 225) recorded using accelerometers over three and half years. Each date is represented as a boxplot denoting the 25 and 75 quantiles with dots representing activity outside that range.

mating season had higher activity than non-breeding males and females (Fig. 3b; $z = 5.57$, $p<0.001$). Among breeding males, activity increased with increasing reproductive opportunities ($z = 2.01$, $p = 0.04$), with indications, although not significant, that the strength of this response might increase as resource availability decreases (Fig. 3b; $z = -0.25$, $p > 0.05$).

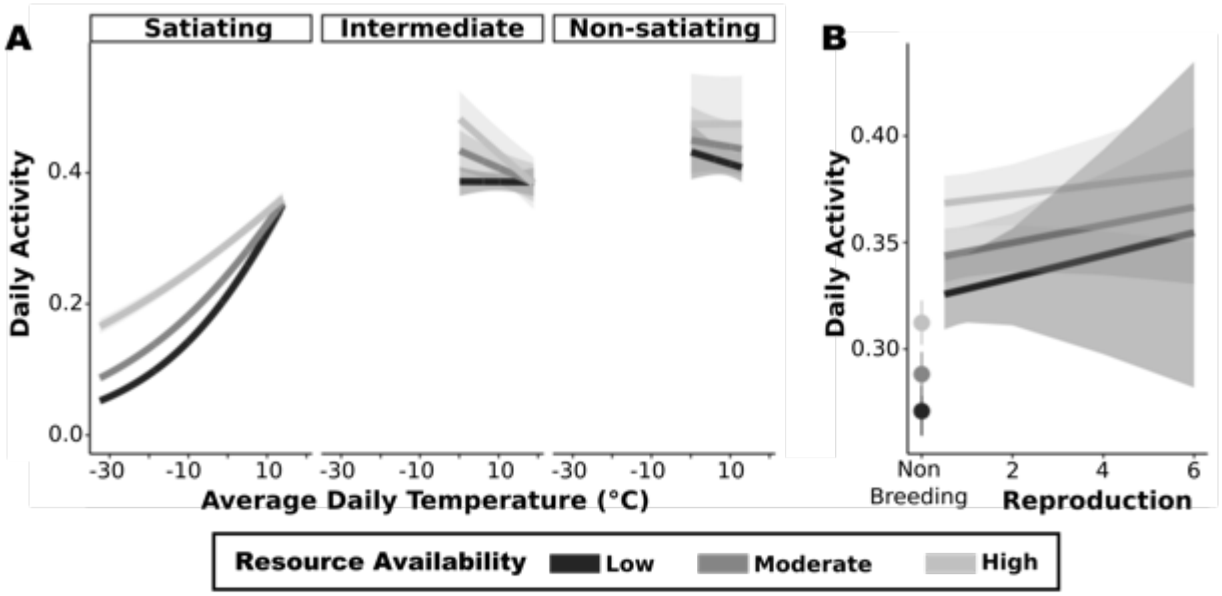

Figure 4.3 Daily activity (proportion of 24 hours) responses to temperature, resources, and reproductive opportunities. The effects of temperature on activity were dependent on resource availability and resource type (A), while the effects of mating opportunities were dependent on resource availability (B). Responses and 95 confidence intervals were generated from a GLMM of 3.5 years of activity data collected from accelerometers. Resource availability at a saturation (R_T) value of 0 are 5 (low), 20 (moderate), 40 (high), while at an R_T of 0.5 and 1 are 60 (low), 90 (moderate), and 120 (high) to represent the natural range observed at each condition. As mating only occurs when $R_T = 0$, resource availability values were 5 (low), 20 (moderate), and 40 (high).

Modelled Activity

Our model predicted that activity increased exponentially as daily mean temperature (T_a)

increased and approached the thermal neutral zone of an endotherm. Increasing resource availability resulted in increased activity but the extent of that increase was dependent on resource type. If no resources were hoardable then there was a moderate increase in activity but as the proportion of hoardable resources increased, the benefits of remaining active began to outweigh the benefits of inactivity, and activity increased towards maximum values. Finally, increasing mating opportunities increased activity. Although these independent responses of activity to temperature, resources, and reproductive opportunities provide general patterns, most organisms live in environments where all three drivers fluctuate simultaneously creating interacting effects on activity (Fig. 4). The model predicted that daily activity was lowest when all resources were non-hoardable and when temperatures were well below the lower critical temperature. Availability of hoardable resources and warm temperatures both increased energetic gain to a point where day-long activity would occur. Resource availability influenced the activity responses to temperature such that the strength of the response to decreasing temperature increased with decreasing resources (Fig. 4a). The effect of mating opportunities was independent of temperature, but dependent on resources with the activity response to mating opportunities increasing with decreasing resource availability (Fig. 4b).

Comparing Measured and Modelled Activity Patterns

Our model with diminishing return values set to the best fit ($\alpha_{\text{Hoardable}} = 1.10 - 1.12$, $\alpha_{\text{Non-hoardable}} = 1.09 - 1.35$) predicted squirrel activity within 1.2 hour of the observed daily mean 59.8% of the time and within 2.4 hours of the mean 92.6% of the time (Fig. 5a, b). Predicted activity values were highly correlated with observed values ($R^2 = 0.83$) suggesting that overall the model accurately captured the seasonal and multi-annual variation in squirrel activity (Fig. 5c).

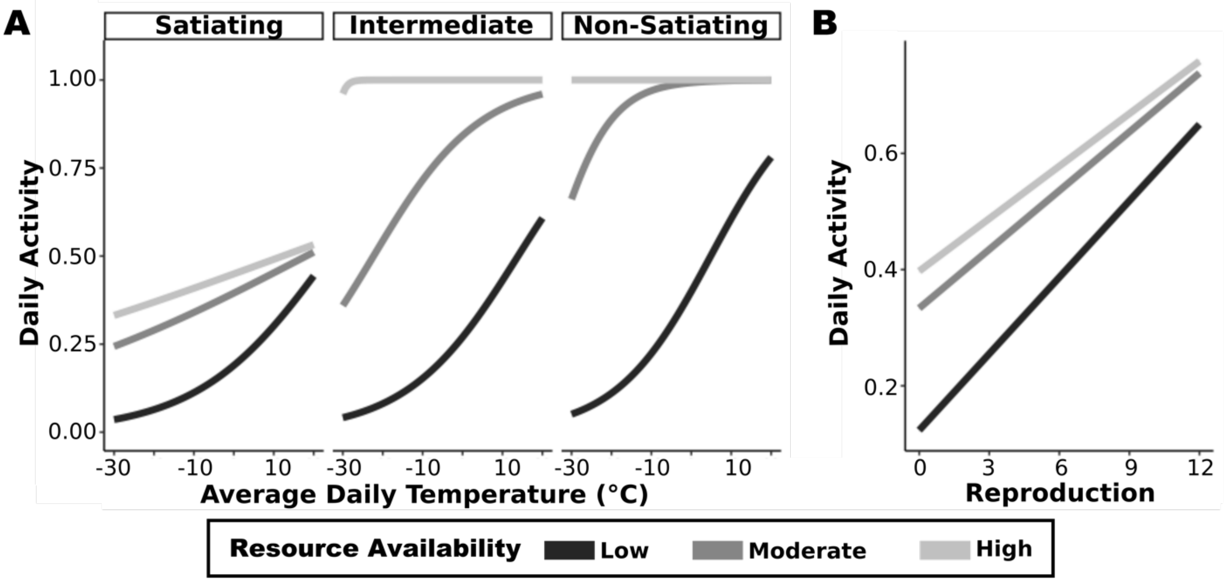

Figure 4.4. Predicted responses of optimal daily activity (proportion of 24 hours) of red squirrels to temperature (A), and reproductive opportunities (B) across variation in resource availability and resource type (panels in A). Predictions are based on measured values of ambient temperature (Ta), resource availability (RA), proportion of available resources that were satiating (RT), and mating opportunities (nq) from the study area.

However, the model tended to over-estimate the lowest activity levels, and failed to capture one period of high activity (spring 2015). Adjusting diminishing return values of hoardable and non-hoardable resources changed the accuracy of predicting activity within 2.4 hours of observed values (accuracy range = 0-0.926 %; Supplementary Materials 5, Fig. S3) but had minimal influence on the correlation between predicted and observed values (R^2 range = 0.609 to 0.83).

Discussion

We demonstrated that the vast majority of multi-seasonal and multi-annual variation in activity can be explained by an energetic-based behavioural choice model that incorporates only resource

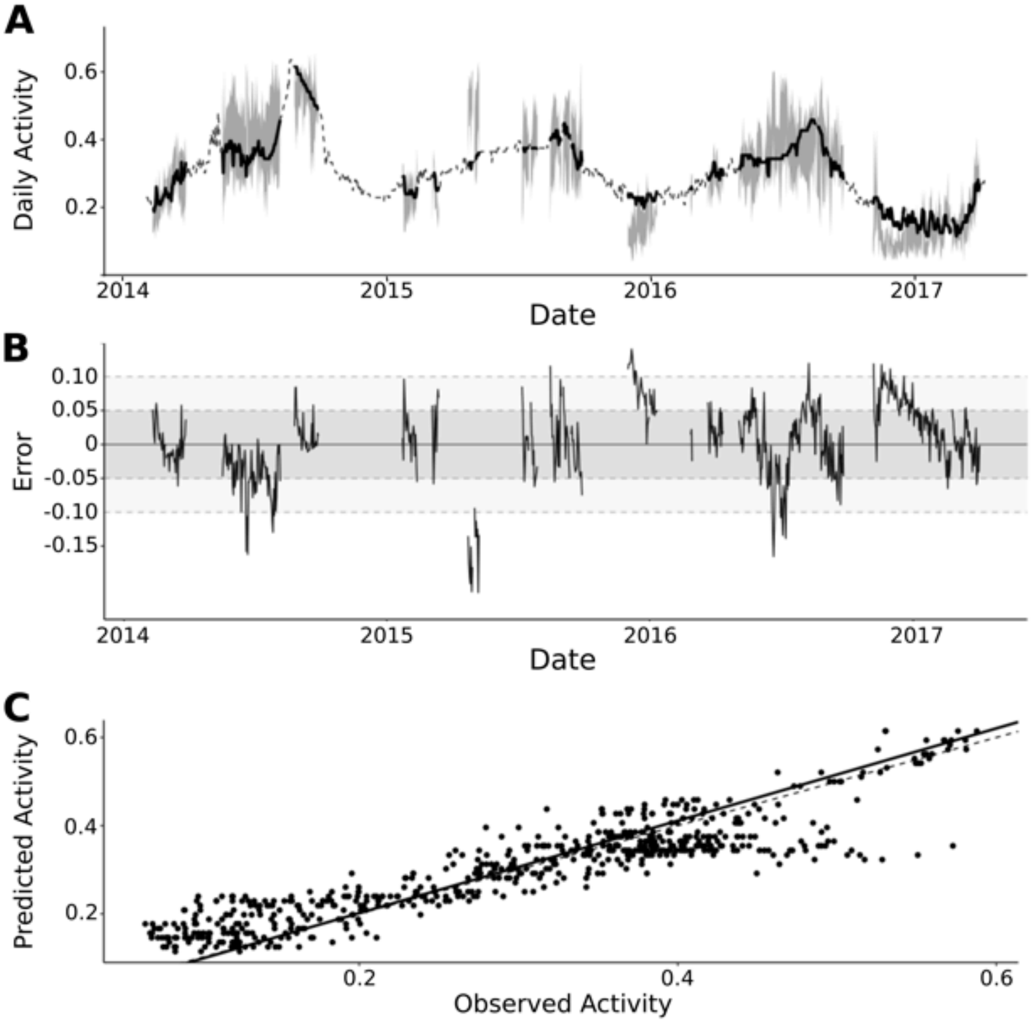

Figure 4.5. Observed and predicted daily activity of a population of free-ranging red squirrels in southwestern Yukon (A). Activity was observed over 3.5 years using accelerometers (n=489) and predicted according to optimization of energetic and reproductive gain in the decision between activity and inactivity. Predictions (black) are overlaid on range of observed daily activity (light grey shading). The correspondence between observed and predicted is assessed by the error of the prediction relative to the observed daily mean value (B), and the correlation of predicted daily values to observed (C). Error of the prediction is the difference between the observed mean daily proportion of activity and model predicted daily proportion (convertible to hours by multiplying by 24; B). Dark grey band represents within 1.2 hours of daily mean value and light grey band represents range within 2.4 hours.

availability and quality, air temperature and presence of mating opportunities. Our analyses suggest that activity reflects an optimization of energetic and reproductive gain, with individuals active when the gains of activity outweigh the gains (or minimization of losses) offered by inactivity. Based on this optimality approach, the activity responses of free-ranging red squirrels to abiotic and biotic drivers became highly predictable, when aggregated at the level of a day.

Incorporating resource type, air temperature, and reproductive parameters into an activity optimization model predicts that activity responds dynamically to environmental conditions. Increasing resources, increasing ambient temperature, or decreasing resource saturation rates all led to increases in activity. However, both red squirrel activity and our predictive model highlighted the inter-dependency of activity responses to temperature and resources. This interacting effect is driven by resources and temperature influencing opposing components of net energy gain (i.e., resources on intake, and temperature on expenditure), and illustrates that organisms can buffer some environmental variability if either intake can be increased or expenditure decreased (King & Murphy, 1985; Boggs, 1992; Williams et al., 2015). An ability to buffer the environment helps to explain why activity responses to resources and/or temperature vary between studies (Fernandez-Duque, 2003; Murray & Smith, 2012; Hall & Chalfoun, 2019)

Among the environmental drivers we considered, resource type appeared to be the strongest driver of activity variation. The energetic value and potential hoardability of different resource types are known to be key components of short term foraging decisions (Pyke et al., 1977; Gerber et al., 2004; Lichti et al., 2017). Our results extend these patterns across much longer time scales, to show how resource abundance and saturation drive daily activity levels across seasons and years. In red squirrels, we distinguished resources according to whether they could be hoarded (i.e., weakly saturating) or not (i.e., strongly saturating) and the model confirmed the importance of this distinction. From an ecological perspective, non-saturating foraging returns for hoardable resources drives high rates of sustained activity for as long as this resource type remains abundant. Although we only focused our categorization of resource type on the distinction between hoardable and non-hoardable resources, additional resource type differences would need to be considered in systems where, for example, energetic values, nutrient composition, or handling constraints vary more and have stronger effects on activity optimization (Emlen, 1966; Pyke et al., 1977; Gill, 2003).

Beyond resources and temperature, reproductive gain associated with mating opportunities is an important driver of activity. Reproduction requires activity for mate searching and courtship in addition to mating itself (Daly, 1978; Real, 1990), and in scramble competition mating systems, like in red squirrels, increased mate searching or activity is linked to increased mating success (Lane et al., 2009). We found that considering reproductive gain as a probabilistic outcome of activity in the model adequately predicted observed activity responses expressed by red squirrels in relation to mating opportunities. This approach meant that activity for mating is not mutually exclusive of that for foraging. Activity that capitalizes on mating opportunities instead of foraging comes at the detriment of energy balance as there is insufficient energy intake to offset the cost of activity (Lescroël et al., 2010; Foley et al., 2018). In red squirrels, the late winter mating season is associated with elevated energy expenditure (Lane et al., 2010) and endocrine indications of stress and energy mobilization (Boonstra et al., 2017).

Despite our model's high predictability of squirrel activity (83%; when diminishing return values were set to best fit), error tended to be concentrated in time and likely results from some shortcomings. First, our model did not account for behavioural responses to predation risk, a critical component of many foraging theories (Brown, 1992; Brown et al., 1999). If increased predation risk reduces activity (Lima & Dill, 1990), then periods when our model prediction overestimated activity (e.g. early winter) may be indicative of short term increases in risk. Unfortunately, we have no information on how predation risk varies within a year in this system. However, our model's generally high accuracy at predicting activity, despite the exclusion of variation in predation risk, suggests that, for red squirrels, predation risk is either a weak driver of daily activity, relatively stable over time, or highly correlated with another driver included in our model, such as temperature or resources. Nevertheless, given the demonstrated importance of spatial and temporal variation in predation risk on activity in many systems (Hughes et al., 1994; Diaz et al., 2005; Lone et al., 2016; Kohl et al., 2018), inclusion of predation risk into our modelling approach would improve its general applicability beyond bottom-up regulated species like red squirrels, to systems where activity is more responsive to variation in predation risk.

A second source of error likely stems from our estimation of resource availability throughout the year. Although we had measurements of larder hoard quantities and spruce cone availability, we estimated timing and relative amounts of all other resources according to snow depth, squirrel diet composition data, and known phenological information (Fletcher et al., 2013). These estimates, although reasonable, likely do not perfectly capture resource availability across seasons and years. Despite this, the error in the model did reveal resource-related behaviour that was previously unknown. Revisiting behavioural observations collected in spring 2015, where our model considerably underestimated activity, revealed that a secondary hoarding season occurred following a spruce masting the previous autumn. As the snow melted, squirrels appeared to reinitiate hoarding behaviour, collecting cones that were buried by snow in the autumn.

Despite its simplicity, we show that energy-based optimality models of behaviour can have a surprisingly powerful ability to predict activity variation expressed by individuals over seasonal and annual time frames. Some of the activity responses to environmental variation described here, like reduced activity in winter, when resources are scarce, days are short, and air temperatures are cold, may seem unsurprising, but are also indicative that behavioural decisions are based on a maximization of energetic gain rather than a maintenance of energy balance (which would cause activity to increase, instead of decrease, as resources or temperature decreases). Our analyses also revealed several, less obvious patterns, including autumn activity peaks driven more by resource type than resource abundance, the resource-dependency of activity responses to temperature and mating opportunities, and activity peaks not predicted by the model used to identify novel, season-specific forms of activity. Additionally, we show that aggregation of behavioural variation to a daily scale was critical to predictive success; our model predicted 83% of variation in daily activity expressed across seasons and years, but if we attempted to predict whether any given individual was active at any given moment, across the same multi-annual extent, explanatory power dropped to less than 15%. It thus appears, that at the scale of days, seasons, and years, the energy and reproductive requirements of populations coalesce with constraints imposed by the abiotic and biotic environment to drive highly deterministic and predictable activity responses. Whereas, within these days and seasons, at the scales of minutes to hours, individuals retain considerable flexibility in choosing what to do and where to be at any one moment in time. Intriguingly, if we as researchers can predict squirrel behaviour using relatively few variables and a relatively simple model, perhaps so too can predators, which presumably know them better. This may cause predators to structure their activity patterns according to these expectations, which in turn may select for variability in behaviour around the central tendencies documented here. This could account for the unpredictability of behavior at finest temporal scales. We hope that the opportunity to combine activity-and energy-explicit optimality modelling with biologging of activity patterns expressed across seasons and years enables broader evaluation of the importance of behavioural variation in seasonal and annual energetic status, population dynamics, and trophic interactions. As also described in Humphries and McCann (2014), this may include extending how we think of metabolic theories in ecology, beyond equations focused on size, temperature, and metabolic rate (Brown et al., 2004), to include equations focused on energy balance, energy flows, and the ecological importance of both metabolic and behavioural variation.

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Linking Statement

In the previous chapter, I showed that activity across seasons and years is highly predictable as the outcome of an optimization of energetic and reproductive gain. With activity mainly being driven by resources, temperature, and mating opportunities, this chapter indicated that all species should be characterized by annual patterns in activity with fluctuations between seasons. The next chapter explores how differential behavioural responses to seasonality impact the flow of energy and biomass within a population through interactions within a food web motif. By incorporating activity into predator-consumer-resource dynamical equations, empirically-support model predictions show how the extent to which a species is seasonally flexible in behaviour impacts the population rate of increase, decrease, and population stability.

Chapter 5 - Bioavailability, ecological dynamics, and the paradox of seasonal enrichment

Summary

Seasonality in northern latitudes is an annual cycle comprised of wavelike variation in photoperiod and temperature that has inevitable and unavoidable impacts on organismal function, ecological interactions, and evolutionary outcomes (Bridgman & Oliver, 2006; Morisette et al., 2009; Steltzer & Post, 2009; Padian, 2012; Basille et al., 2013; Dopico et al., 2015; McMeans et al., 2015). Whether seasonality maintains or constrains biological diversity depends on the extent and consequences of differential responses to seasonal variation (Hurlbert & Haskell, 2003; Tonkin et al., 2017). Here we focus on a subtle but ubiquitous form of differential responses to temporal variation – the behavioural switch between active and inactive states – that leads to covariation in energy intake, energy expenditure, and predation risk (Anholt & Werner, 1995; Humphries & McCann, 2014). This behavioural switch defines how individuals engage with environmental variation, and determines the bioavailability of populations within food webs. We develop energy- and activity-explicit consumer-resource equations to examine the seasonal dynamics of a food web motif consisting of a predator and two consumers that have different behavioural flexibilities to seasonality. Predators optimizing seasonal prey choice will have diverse diets in summer when warm temperatures and abundant resources cause high activity in more behaviourally-flexible consumers, and more specialist-like diets of less behaviourally-flexible consumers in winter, when cold temperatures and scarce resources cause more flexible consumers to become less active and more decoupled. As a consequence, less flexible consumers experience intense predation in winter, but also a critical respite from predation in summer when predators switch back to bioavailable more flexible consumers.

Seasonality is thus essential to the coexistence of both types of consumers and their generalist predators, and changes in the duration and severity of seasons will disrupt the balance of seasonal advantages and disadvantages. Because less flexible consumer's respite from predation occurs during the productive summer season and more flexible consumers must allocate a substantial fraction of summer production to winter maintenance, less flexible consumers should be characterized by a higher realized rate of increase during summer and higher losses to predation during winter relative to more flexible species characterized by dampened seasonal dynamics. A well-characterized vertebrate food web in a highly seasonal boreal environment generates empirical support for most model predictions, as does a global analysis of the population dynamics of small mammals expressing extremes of differential seasonal activity. As summers continue to lengthen and winters become less severe, empirically-supported theory predicts amplified rather than diminished seasonal dynamics, extending the paradox of enrichment to a seasonal realm.

Main Text

Behaviour, seasonality, and, especially, differential behavioural responses to seasonality are rarely considered, but likely important, drivers of ecological dynamics. Behaviour can be defined as choices made by whole organisms, which have purpose and take time (Baum, 2013, see also Levitis et al., 2009). Among the many axes of behavioural variation, the decision to be active or inactive is a choice and an optimization outcome that defines the trophic status of individuals and populations by determining co-variation in energy intake and expenditure, foraging behaviour and vulnerability to predation, and environmental exposures and refuge occupation (Studd et al., in review). Activity optimization is thus both a trait-mediated indirect interaction (Werner &

Peacor, 2003) and a non-consumptive effect (Peckarsky et al., 2008). Here we test the hypothesis that activity plays a key role in the seasonal balance of energy within individuals, species, and food webs, with high activity associated with high intake, high loss, and strong interactions, and low activity associated with low intake, low loss, and weak interactions. We also extend consideration of the paradox of enrichment – the tendency towards ecological instability in resource-rich environments (Rosenzweig, 1971; Tabi et al., 2019) – to a seasonal realm.

Co-occurring species experiencing the same climate conditions can be characterized by highly differentiated seasonal activity responses. Hibernation - literally to spend winter in an inactive state - represents the extreme of seasonal flexibility, combining energy storage (often high in quality and quantity) with metabolic depression, permitting winter-long inactivity and trophic decoupling (Withers & Cooper, 2010; Williams et al., 2016; Humphries et al., 2017). But even among non-hibernating mammals activity patterns can be strongly differentiated. Our monitoring of activity over four years with accelerometers on North American red squirrels (n = 225) and snowshoe hares (n = 127) illustrates the differential behavioural flexibility of two homeothermic herbivores experiencing the same highly seasonal boreal environment (Fig. 5.1). Red squirrels, that consume high-quality seed that is made accessible year-round via food hoarding, have seasonally flexible activity (i.e. low activity in winter, high activity in late summer; Fig. 5.1). Meanwhile, snowshoe hares that consume relatively low quality vegetative tissue are characterised by higher overall activity than squirrels and dampened seasonal variation (Fig. 5.1).

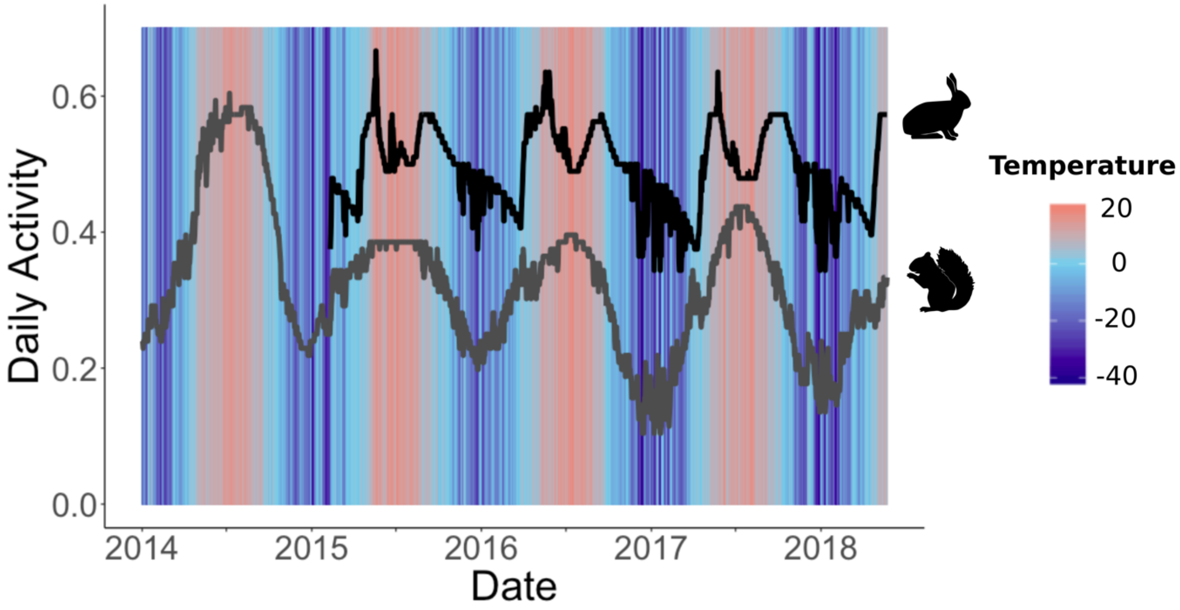

Figure 5.1. Seasonally differentiated daily activity of co-occurring red squirrels (dark grey) and snowshoe hares (black) at Kluane, Yukon. Background colour reflects daily air temperature variation, ranging from -40°C indicated by the darkest blue to 20°C indicated by the brightest red. Predicted activity of both species is generated from an optimization model (Studd et al., n.d.) that had high accuracy at matching observed range of values collected using accelerometers (squirrels = 0.76 %, hares = 0.81 %).

Because activity is energetically costly and is a pre-requisite for energy intake, seasonal activity patterns define the seasonality of biomass production. Consider the ability of an individual or a population to acquire an energetic surplus, S, through rates of intake, I, that exceed rates of energy expenditure, E.

$$S = I - E \qquad \textit{eq. 1}$$

Given activity, p, is necessary for intake (Schoener, 1971; Abrams, 2010), and energy expenditure when active, e_a, exceeds expenditure when inactive, e_m, by an activity multiplier, A (Karasov, 1992; Alexander, 2005) then:

$$S = p(I - e_a) - (1 - p)e_m = p(I - Ae_\mathrm{m}) - (1 - p)e_m \qquad \textit{eq. 2}$$

Summer provides a seasonal window of opportunity for high rates of production, particularly in herbivores, for which resource availability tends to be high due to elevated primary production, and particularly for endotherms, for which energy requirements tend to be low due to thermally neutral ambient temperatures. However, the situation reverses in winter when low primary production limits resource intake and cold air temperatures increase maintenance requirements. While the capacity for some species to avoid this winter energetic bottleneck through reduced activity or hibernation is well described (see Lovegrove, 2000; Ruf & Geiser, 2015), an under-recognized consequence of this seasonal decoupling is the need to allocate a fraction of summer production to energy storage in order to offset winter deficits (Fig. 5.2a). As a consequence, seasonally flexible species that reduce activity in winter are predicted to have lower rates of maximum summer production than seasonally inflexible species remaining active throughout winter (Fig. 5.2b). Within the boreal forests of Kluane, Yukon, Canada, where spring and autumn densities of snowshoe hares and red squirrels have been monitored for the past 30 years, snowshoe hares characterized by high winter activity exhibit higher summer biomass production rates than red squirrels that reduce activity in winter (unpaired t-test, $t = 3.9332$, $df = 31.567$, $P < 0.001$; Fig 5.2c). This trend extends beyond these two species at Kluane, including red-backed voles that express year-round constancy in activity levels (Stebbins, 1972) and are characterized by high rates of summer production, and arctic ground squirrels that hibernate (Williams et al., 2012) and have low rates of summer production (Supplemental Fig S7.5.1). This pattern also extends beyond the boreal forest, with global analyses indicating hibernating mammals have lower production rates than non-hibernating species (Kirkland & Kirkland, 1979).

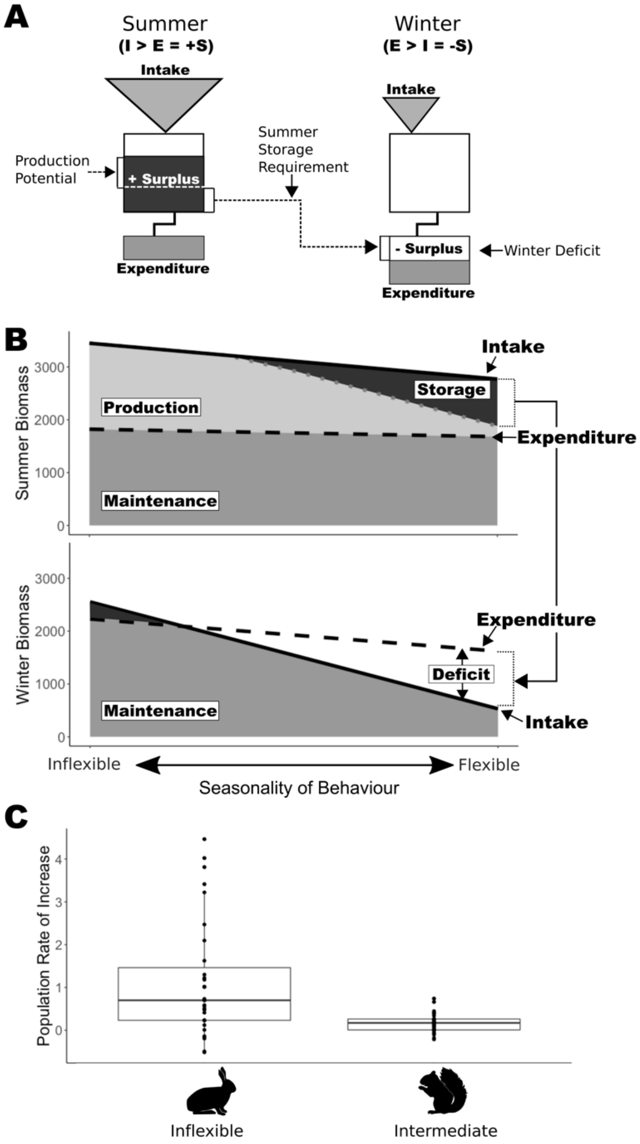

Figure 5.2. An extension of Weiner's barrel model of energy balance to a seasonal realm (a). In summer, the intake triangle is large and energy expenditure (bottom) is low resulting in a highly positive energy balance (black fill). In winter, intake is lower, expenditure is higher, and balances are negative (deficit). Summer production potential is gain above expenditure minus summer storage, which is equivalent to winter deficit. Model predicted energy balance (b) in summer (top) and winter (bottom), along a seasonality of behaviour continuum (inflexible express year-round constancy in activity, flexible express high activity in summer and low to no activity in winter). Although the flexible end of the continuum is just as active in summer, their potential rates of production are less, because they need to store summer accumulation for winter deficits. Observed rates of spring to autumn increase (c) over 30 years for snowshoe hares, which

are characterized by inflexible activity, and red squirrels, which are characterized by seasonally flexible activity

Given activity also affects vulnerability to predation, a predator's prey selection and consumption rate will vary not just with the biomass of each prey species, but also their activity levels. We refer to this activity-adjusted biomass measure as bioavailability, B, and assume

$$B = pV_{\mathrm{a}} + (1 - p)V_{\mathrm{i}} \qquad \text{eq. 3}$$

where V_a and V_i are vulnerability to predation when active and inactive respectively. The optimal prey choice of a predator, P, between two consumers C_1 and C_2 is thus

$$\boxed{\Omega_{PC_1} = \frac{\omega_{C_1} C_1 B_{C_1}}{\omega_{C_1} C_1 B_{C_1} + (1-\omega_{C_1}) C_2 B_{C_2}}} \qquad \text{eq. 4}$$

where $\boxed{\Omega}$ is the proportion of the predator's diet made up of one consumer, $\boxed{\omega}$ is the preference of the predator for consumer 1 over consumer 2, and C is the biomass of the consumer. If the seasonal activity patterns of the two consumers differ, with C_i expressing seasonally inflexible behavior and C_f expressing high activity in the summer and reduced activity in the winter, then predators are predicted to consume primarily C_i when C_f is inactive, but as C_f becomes more active, broaden their diets to include both species (Fig. 5.3a). The seasonality of lynx predation on less behaviourally flexible snowshoe hares and more behaviourally flexible red squirrels, quantified over three winters using lynx-attached acoustic recorders, provides direct support for this prediction (Fig. 5.3b). Lynx consumption of snowshoe hares and red squirrels varied with red squirrel activity, with consumption of red squirrels at its lowest rate (0% of 79 kills) during the winter months (Jan-Feb; Fig. 5.3b) when squirrels are least active (Fig. 5.1a), and increasing in autumn and early spring (~30% of 64 kills) when squirrel activity increases (we lack data on lynx prey consumption in summer and autumn when squirrels are most active because we have so far captured lynx only in winter months and acoustic recorders have limited battery life).

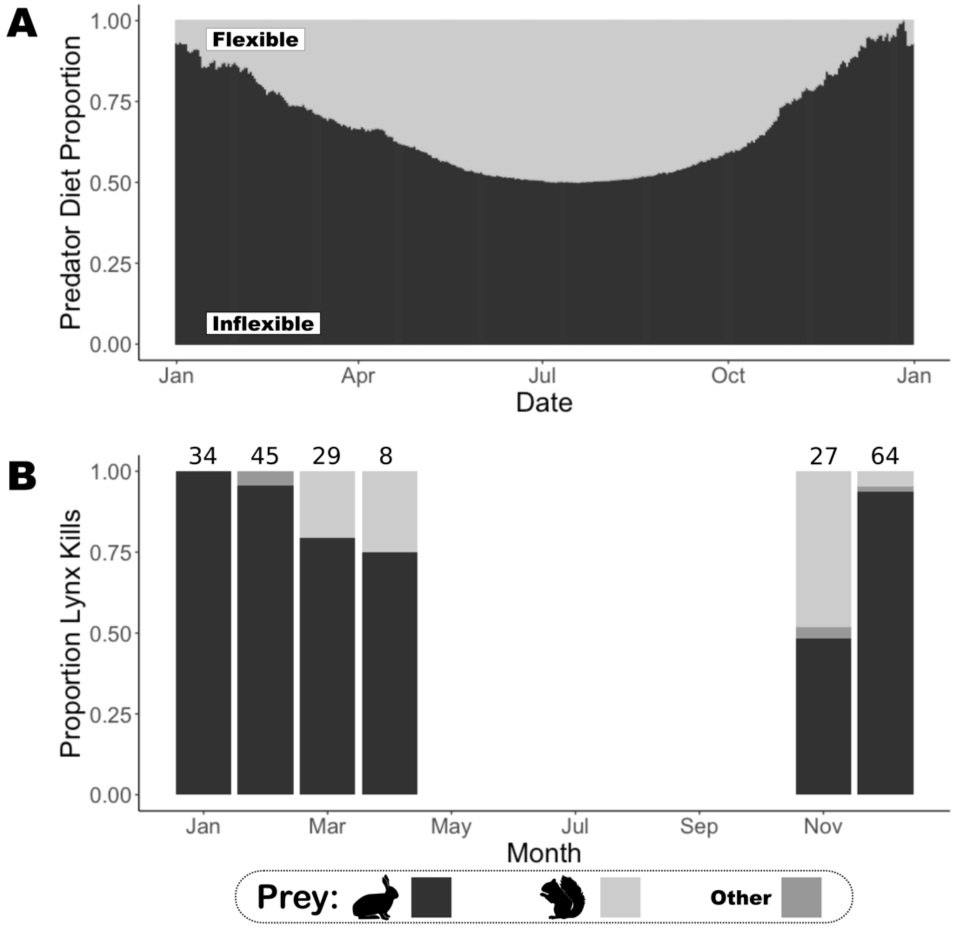

Figure 5.3. Predator diet composition is dependent on the activity of the prey. Model predictions of predator diet (a) on two prey species at equal biomass illustrate a seasonal shift in diet in response to the bioavailability of the flexible prey species. Canada lynx diet composition of inflexible (snowshoe hare; black) and flexible (red squirrel; light grey) prey species calculated from animal-borne acoustic recorders shows a seasonal transition in response to the activity of the flexible prey. Numbers on top of bars are the total number of kills recorded each month.

As a result of predators switching between prey according to their bioavailability, consumer populations characterized by high and seasonally invariant rates of activity should experience high predation rates and mortality in winter when seasonally flexible species are inactive and therefore unavailable to predators. In return, these same consumers should experience a reprieve from predation in summer, when seasonally flexible species increase their activity and bioavailability to predators. This seasonal switch of bioavailability and predation can be modeled by expanding eqs. 2-4 into energy- and activity-explicit dynamical equations that consider the flow of biomass and energy (Yodzis & Innes, 1992; McCann et al., 1998) between a predator, P, and two non-competing consumers, one of which expresses seasonally flexible activity, C_f, and one characterized by behavioural inflexibility, C_i, and thus seasonally constant activity. The complete set of dynamical equations and parameters are described in the methods. This model predicts that seasonally flexible species will have the highest mortality in the summer when their activity is high, and the lowest mortality in winter when their activity is low, whereas seasonally inflexible species will have the highest mortality rates in winter when flexible species are inactive, and the lowest mortality rates in the summer when flexible species are active (Figure 5.4a). Daily monitoring of snowshoe hare survival, conducted year-round over 4 years using VHF collars equipped with mortality switches (Peers et al., submitted), indicates that mortality rates within this consumer with low behavioural flexibility were indeed highest in the winter and near zero in the summer (unpaired t-test: $t=9.06$, $df=171$, $p<0.001$; Fig. 5.4b). Meanwhile, red squirrels, present in the same habitat and being preyed upon by the same predator guild as snowshoe hares but characterized by reduced activity in winter, experienced higher adult mortality rate in summer than winter (paired t-test: $t = 4.771$, $df = 26$, $p < 0.001$, Fig. 5.4c), as estimated through bi-annual population censuses conducted every spring and autumn for 27 years. Beyond these relative seasonal differences, both maximum and annual average mortality rates were substantially higher in snowshoe hares, the C_i, than red squirrels, the C_f. The model did not, however, predict that snowshoe hare mortality would decline to near zero in summer.

This discrepancy may arise from our mortality monitoring of only adult hare survival during a summer reproductive season when predators may switch to more vulnerable newborn and juvenile hare age-classes, as well as the multiplicity of C_f populations present in this system in the summer.

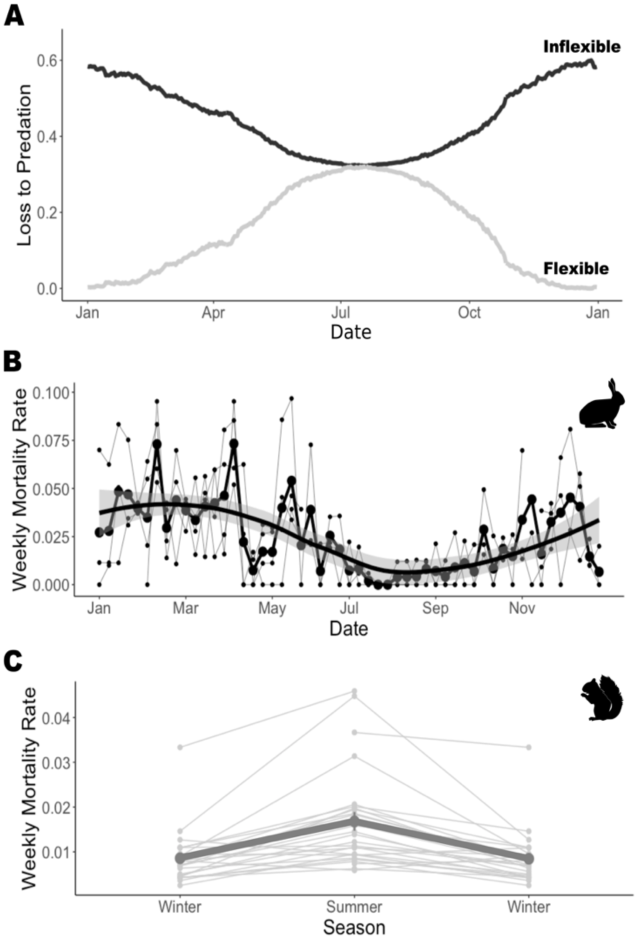

Figure 5.4. Seasonal shifts in predator prey choice due to changing bioavailability generates differential mortality rates over the year for behaviourally inflexible (black) and flexible (light grey) prey. Model predictions (a) suggest that inflexible prey will have higher mortality in winter than summer while flexible prey will higher mortality in summer than winter. Weekly mortality rates of inflexible adult snowshoe hares (b) calculated from individuals monitored daily for four years, and flexible adult red squirrels (c) calculated from individuals monitored seasonally for 27 years illustrate this pattern empirically. For empirical data values from each year of the study are shown in the background with the mean values across the whole study in the foreground.

Given inflexible consumers produce high amounts of biomass in summer and lose substantial biomass to predation in winter, while flexible consumers gain less in summer but also lose less in winter, one might expect that these seasonal differences cancel out on an annual basis, causing the two strategies to have similar multi-annual rates of increase and population dynamics. But, according to theory, C_f and C_i are in fact predicted to differ substantially in multi-year dynamics because C_f must allocate a substantial portion of summer production to storage (to offset winter deficit) and because C_i experiences a reprieve from predation during the most productive phase of the annual cycle. Flexible species are predicted to be characterized by dampened annual rates of increase and decrease, which are less affected by predator densities, relative to inflexible species with more divergent rates of increase and decrease that also vary more with predator density (Fig. 5.5a). As a consequence, inflexible species exhibit less multi-annual population stability and are more likely to express cyclic dynamics than flexible species (Fig. 5.5b). To test this prediction empirically, we calculated maximum rates of increase and decrease, and population coefficient of variation for 299 small mammal time series included in the Global Population Dynamics Database (NERC Centre for Population Biology Imperial College, 1999). Within this sample, we consider species described as hibernators to be the most seasonally flexible, species that do not hibernate but express torpor as intermediately flexible, and year-round homeotherms as the least seasonally flexible. Within these homeotherms, positioned toward the inflexible end of the continuum, homeotherms consuming seeds and other plant reproductive structures tend to express more seasonal flexibility, related to the hoardability and seasonality of these food sources, than homeotherms consuming vegetative plant parts and insects. Across the 57 species in the database, we found that species that hibernate, express torpor, or are homeothermic consumers of seeds and other reproductive plant structures tend to have, although not significant, dampened population increases and decreases (increase: ANOVA F=2.4, df=4, P=0.0619; decrease: ANOVA F=1.4, df=4, P=0.237; Fig. 5.5c) and more stable population dynamics (ANOVA, F=5.564, df=4, P<0.001; Fig. 5.5d) than homeotherms, consuming insects or vegetative plant parts.

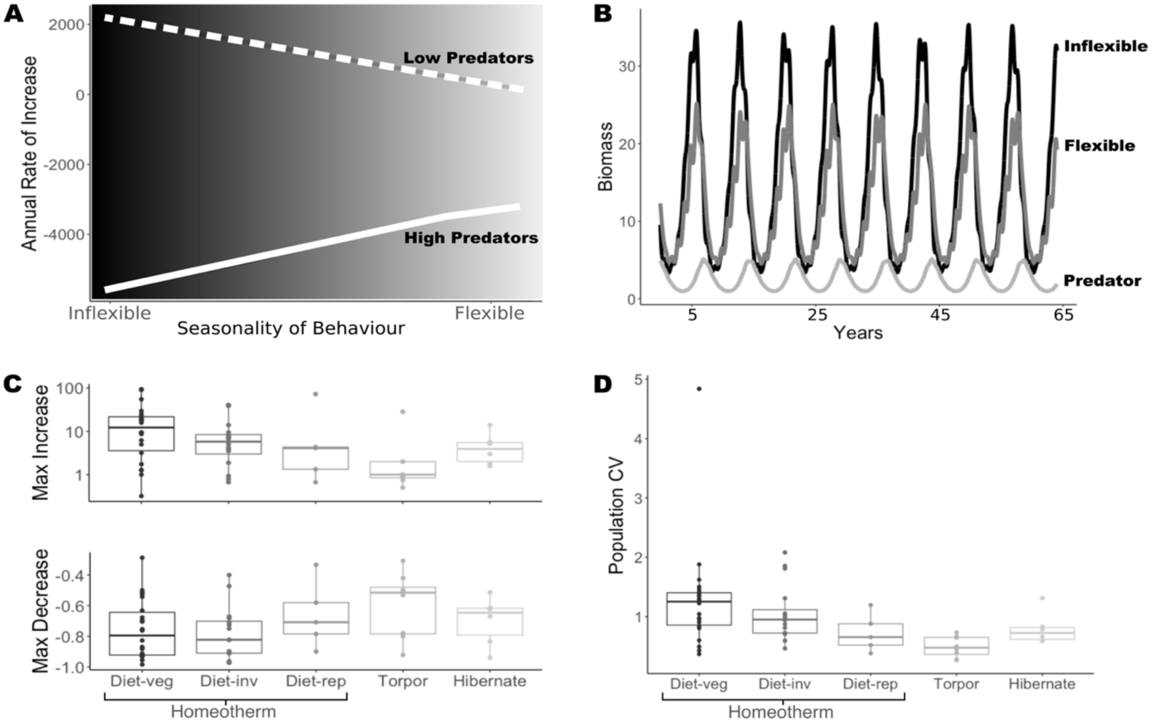

Figure 5.5. Annual rate of increase, decrease and population stability depend on the flexibility of behaviour to seasonal variation. Model predictions (a) show that behaviourally inflexible consumers will have higher rates of increase when predators are scarce and higher rates of decrease when predators are abundant than flexible consumers, which produces larger amplitudes in population dynamics (b). Analysis of population time series from 229 small mammal populations illustrates that observed maximum rates of increase and decrease are more extreme (c) and population coefficient of variation are greater (d) for diet and thermoregulatory strategies associated with behavioural inflexibility than more flexible strategies. Shading of boxplots range from behaviourally inflexible (black) to flexible (light grey) species. Diet categories include plant vegetative material (veg), plant reproductive material (rep), and invertebrates (inv).

Given the seasonality of behaviour influences the balance of seasonal biomass gains and losses as well as multi-annual population dynamics, climate change towards milder winters and longer and warmer summers (IPCC, 2013) should have differential effects on behaviourally flexible and inflexible consumers. We assessed how changes in winter frequency of days below -15°C and summer growing degree days influence the population dynamics of inflexible and flexible species by comparing model predictions to observed seasonal dynamics of snowshoe hares (less flexible) and red squirrels (more flexible) over 30 years of varying climate conditions. Model predictions suggested minimal influence of longer, warmer summers on the summer biomass gain of flexible or inflexible species (Fig. 5.6a) and empirical population data show weakly positive or no relationships among these variables. Theory predicted a strong effect of predator density on summer biomass gains of both consumer types, but empirically only inflexible hares showed reduced summer gains under conditions of high predation (Fig. 5.6b). In contrast, theory predicted less severe winters would lessen winter biomass loss in the inflexible consumer, but not the flexible consumer (Fig. 5.6c). Empirical data supported this prediction with less flexible snowshoe hares being characterized by less biomass loss in the least severe winters, under both low and high predation circumstances, whereas the winter biomass loss of more flexible red squirrels was unrelated to winter severity or predator abundance (Fig. 5.6d). This suggests that as summers lengthen and warm, and winters become less severe, the balance of competitive advantage between seasonally flexible and inflexible consumers shifts towards the inflexible strategy as their production is maintained or slightly increased during summer, and conserved much more during winter. This expectation that less severe winters and warmer summers will benefit inflexible species more than flexible species is surprising given inflexible species seem to be best adapted to cope with severe winter conditions (to which they are exposed as a result of their inflexibility) and best positioned to capitalize on the summer reprieve from predation (resulting from the increased summer activity and bioavailability of flexible species). Given inflexible species express much larger seasonal biomass amplitudes and destabilized multi-annual dynamics, an even more surprising outcome is that as seasonality of the environment diminishes, the seasonal biomass fluxes and the dynamical instability of dominant consumers is predicted to amplify. We refer to this expectation as the paradox of seasonal enrichment.

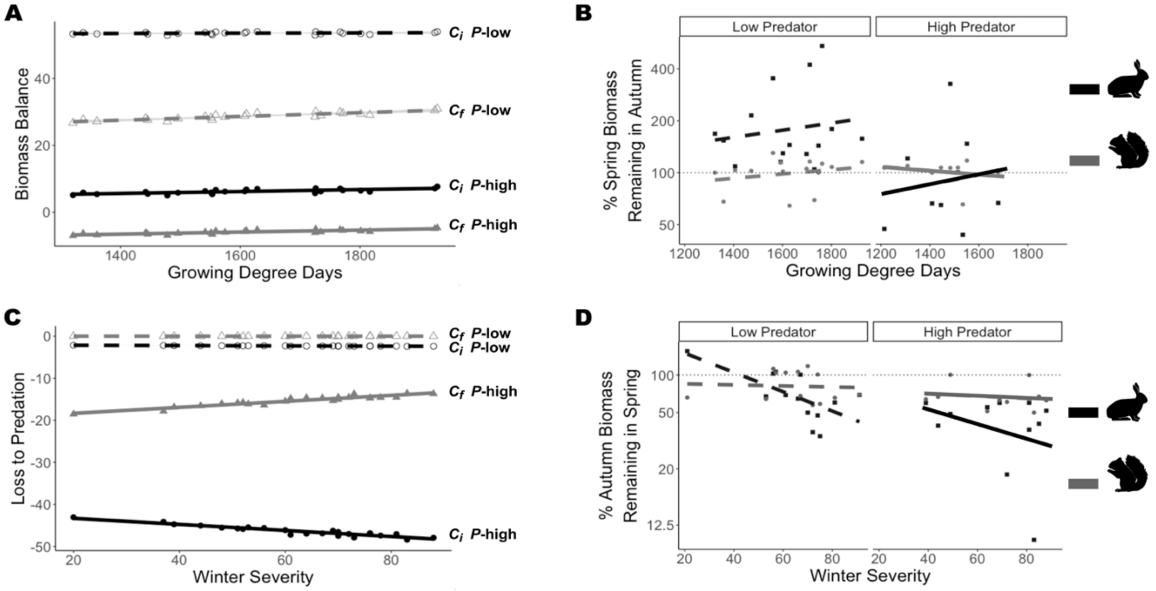

Figure 5.6. Predicted values and observations of biomass production across the variation of summer and winter intensities observed in Kluane between 1995 and 2018. Predictions of the influence of growing degree days (a) and winter severity (c) on biomass production of behaviourally flexible (C_f) and inflexible consumers (C_i) when activity varies with temperature. The effect of condition is dependent on whether there are no predators (dashed; P-low) or abundant predators (solid; P-high) in the system. Observed summer (b) and winter (d) biomass changes of snowshoe hares (black), red squirrels (gray) according to growing degree days and winter severity. Low predator condition were years during the hare population increase, and high predator condition were years during the hare population decline. Growing degree days was the accumulated temperature of all days > 5°C between April 1 – and Oct 31. Winter severity is the number of days during winter when temperature was < -15°C.

Energy- and activity-explicit population biomass models, the seasonal activity patterns of boreal vertebrates, and their seasonal and multi-annual population dynamics, supports the following conclusions. First, consumer species present in the same place at the same time, and therefore experiencing the same seasonal variation in environmental conditions, can be characterized by highly differentiated seasonal responses and a range of activity flexibility. These activity patterns and differential responses appear to be related to dietary differences and the seasonal availability of preferred resources, which extend to more generalized differences in organismal design spanning physiology, behaviour, life history, and natural history. Second, the maximum potential rate of increase and decrease for a population is determined by its seasonal activity patterns and those of all other interacting species in the system. From this we suggest that differences in the seasonality of activity provides at least a partial answer to what Myers (2018) describes as one of nature's great mysteries - why some species cycle and others in the same environment do not. In short, species that cycle are characterized by seasonally invariant activity and constant trophic-coupling, while species that do not cycle are characterized by seasonal inactivity and periodic trophic decoupling. Third, seasons are fundamentally coupled – energy balance in one season determines energy balance in another, and as such understanding processes in one season ultimately requires studying processes in all seasons. By documenting the seasonal, year-round, and multi-annual energy balance of interacting species, we have shown how winter activity and energetic status affects summer biomass production, and the consequences this has on population dynamics. Fourth and finally, we have predicted a paradox of seasonal enrichment, by suggesting that as the extremes of seasonality are diminished by climate change, the magnitude of seasonal biomass fluxes and the instability of biological communities may amplify.

Methods

The Model

We based our model on one proposed by Humphries and McCann (2014) that intake requires activity and activity requires energy such that the total energy flowing through a system can be represented as

$$S = p(I - e_{\mathrm{a}}) - (1 - p)e_m \qquad \text{eq. 2}$$

where S is the surplus energy, p is the proportion of a time period spent active, I is intake, e_a is energy expenditure when active, and e_m is energy expenditure when inactive. Given that energy expenditure is temperature dependent when outside the thermal neutral zone of a species (Scholander et al., 1950), e_a is

$$e_a = -Ac_a(T_b - T_a) \qquad \text{when } T_b < T_{LC} \qquad \text{eq. 5}$$

$$e_a = -AM_{RMR} \qquad \text{when } T_b >= T_{LC}$$

where A is the activity multiplier, c_a is the rate at which metabolic rate increases per degree in temperature, T_b is body temperature, T_a is air temperature, T_{LC} is the lower critical temperature, and M_{RMR} is the metabolic rate when resting. Given that most species utilize some type of thermal refuge when at rest, e_m can be represented as

$$e_m = -(c_{\mathrm{a}} - c_{\mathrm{a}}Q)(T_{\mathrm{b}} - T_{\mathrm{a}}) - c_{\mathrm{a}}Q(T_{\mathrm{b}} - T_{\mathrm{LC}}) \qquad \text{when } T_b < T_{LC} \qquad \text{eq. 6}$$

$$e_m = - M_{\mathrm{RMR}} \qquad \text{when } T_b >= T_{LC}$$

where Q is the refuge quality and ranges from 0 (no thermal refuge) to 1 (refuge maintains temperature within the thermoneutral zone).

Our dynamical equations were formed by merging eqs. 2 and 4 into a two consumer, one predator dynamical system modified from McCann et al. (1998):

$$\boxed{\frac{dC_1}{dt} = \left(1 - \frac{C_1}{K_{C_1}}\right)\left(p_{C_1}C_1\left(I_{C_1R_1} - e_{aC_1}\right) - \left(1 - p_{C_1}\right)C_1 e_{mC1} - \left(\frac{\Omega_{PC_1}C_1 I_{PC_1}}{\Omega_{PC_1}C_1 + (1 - \Omega_{PC_1})C_2 + C_o}\right)P\right)}$$

$$\boxed{\frac{dC_2}{dt} = \left(1 - \frac{C_2}{K_{C_2}}\right)\left(p_{C_2}C_2\left(I_{C_2R_2} - e_{aC_2}\right) - \left(1 - p_{C_2}\right)C_2 e_{mC2} - \left(\frac{(1 - \Omega_{PC_1})\, C_2 I_{PC_2}}{\Omega_{PC_1}C_1 + (1 - \Omega_{PC_1})C_2 + C_o}\right)P\right)}$$

$$\boxed{\frac{dP}{dt} = P p_P\left(\left[\frac{\Omega_{PC_1}C_1 I_{PC_1} + (1 - \Omega_{PC_1})\, C_2 I_{PC_2}}{\Omega_{PC_1}\, C_1 + (1 - \Omega_{PC_1})C_2 + C_o}\right] c_P - e_{aP}\right) - \ (1 - p_P)Pe_{m_P}} \qquad \text{eq. 7}$$

where *K* is the carrying capacity of the consumers, *I* is the maximum ingestion rate given 100% activity, C_o is the half saturation densities for the predator.

For all simulations we set predators to have no preference for one consumer over another ($\boxed{\omega}$ = 0.5), vulnerability of inactive consumers was 0, vulnerability of active consumers was 1. *I* for both consumers was seasonally forced with the summer values being based on the average NDVI measurements of the northern boreal forest, and winter values peaking at the first frost and decreasing consistently through the winter until green-up the following spring. Consumers were treated as identical in all capacities (c_a=0.005, T_b=38, M_{RMR}=0.19, T_{LC} = 0, C_1=C_2) except activity. Activity was considered to be a linear function of temperature with the maximum value (0.6) being equal in all consumers and occurring at the warmest temperatures. Flexibility was quantified by the extent to which activity reduced below this maximum value with decreasing temperatures with flexible species varying between 0.1 – 0.6 within a year. Temperature was the daily mean value from the nearest weather stations to the Kluane field site (1986-1994 Burwash Landing, 1994-2018 Haines Junction, Environmental Canada).

Red squirrel and snowshoe hare seasonal activity patterns

We used accelerometers to measure activity on 225 individual red squirrels over three and a half years (2014-2017, deployments = 489; squirrel-days = 5066) and 127 individual snowshoe hares over four years (2015-2018, deployments= 279, hare-days=14,487) spanning seasonal and multiannual variation in the environment. Individuals were captured on defended territories (squirrels) or at systematically placed trapping locations (hares), and fitted with an accelerometer (models Axy2/Axy3, 4 g [1.7% of body mass], Technosmart Europe) in the form of a collar, either ventrally mounted on its own (squirrels: n=128) or dorsally-mounted in combination with a ventrally-mounted VHF radio transmitter (squirrels: n=361, model PD-2C, 4 g [1.7% of body mass], Holohil Systems Limited, Carp, ON, Canada; see Studd et al., 2019 for collar design; hares: Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada; <40 g, <5% body weight). All animals were released at site of capture and remained free-ranging until recaptured for collar removal or until they were predated on. All procedures were approved by animal care committee at McGill University (Animal Use Protocol #4728) and were conducted under Yukon Territorial Government *Wildlife Research Permits* and *Scientist and Explorers Permits.*

All accelerometers recorded acceleration between +/- 8 g_{forces} at a sampling rate of 1 Hz (all squirrels and 256 hares) or 10 Hz (23 hares). All 10 Hz recordings were down sampled to 1 Hz For squirrels, data was processed and classified into six behavioural states (in nest not moving, in nest moving, out of nest not moving, travelling, feeding, and other (primarily foraging)) according to Studd et al.'s (2019) classification methodology. For hares, data was classified into four behavioural states (not moving, foraging, travelling, and sprinting) using the classification methodology developed by Studd et al (2019). For both species we combined active behavioural states (feeding, foraging, and travelling) together to calculate daily activity as the proportion of 24 hours in which individuals were active (see supplemental materials Figure S7.5.2).

Seasonality in lynx prey selection

Canada lynx were live-trapped between November and April over three years (2015-2018). Lynx over 7 kg were given a GPS collar (Telemetry Solutions remote download model (350g) or Followit Iridium GPS (400g)) with externally mounted self-powered acoustic recorder (EDIC-mini tiny E60-1200h; 50g). For a subset of lynx, GPS data was downloaded throughout the study, and all locations from the previous two days were visited to find kill sites. If tracks were of a feeding event, we identified the prey species, and whether it was a kill (only fresh tracks, signs of a chase), or scavenging (killed by other predator or older snow tracks) event. When snow conditions permitted, we followed lynx tracks between locations and recorded any additional kill sites or chases that occurred.

Acoustic recorders were programmed to record continuously at either 16000 Hz with 2-bit compression, or 8000 Hz with 4-bit compression, recording for up to 25 days. A subset of lynx audio files (24 of 104, 29.25 days) were listened to and transcribed in entirety, recording the start and end time of each sound, what the sound was perceived to be, and whether it was generated by the lynx or by the environment (e.g., other lynx, species, vehicle, wind). This identified that feeding, chasing, sleeping, and vocalizing generated unique and distinguishable sounds that were unlikely to be mistaken for anything else. To identify all feeding events, audio files were loaded in an audio program that visualizes the waveform. Each file was then scanned by listening to five seconds every 5 minutes where sound was generated for more than 1 minute. When the sounds of feeding were identified, we recorded the duration of the event. We validated that the sound identified as feeding was actually feeding in two ways: 1) with snow tracking data, we calculated the percent of kill sites that corresponded to this sound and the percent of feeding sounds that occurred where no kill site was found, and 2) extracted the sound from three videos recorded of free-ranging lynx feeding from behavioural observations during the study to confirm that this was the same sound as what we identified. We determined the prey species being consumed either by the vocalization of the prey when being killed (97 of 207 kills, 46.9%) or by the duration of the feeding event. A combination of direct observations of feeding in the field and those recordings where species was identified by vocalization suggested that duration of consumption of a red squirrel was between 7 and 14 mins (mean = 8.5 mins) while consumption of snowshoe hares was between 18 and 67 mins (mean = 36.8 mins). As only 7% of hare kills had feeding durations less than 20 min, we classified all unknown feeding events with durations less than 15 mins as red squirrel and all feeding events with durations greater than 15 mins as snowshoe hares.

Seasonality in hare and squirrel mortality rates

We monitored hare survival on a subset of the population daily between October and June, and biweekly between July and September. Detailed methods are described in Peers et al (submitted) but are briefly explained here. From February 2015 to June 2018, we captured and collared snowshoe hares (n = 474) with VHF transmitters that had built in mortality signals. Hares were released at capture site and collars remained on individuals until they were predated. Each day all collar signals were checked from set locations in the study area and signal type (live or mortality) was recorded. All mortality signals were investigated and cause of death was determined. We monitored an average of 74 hares (range: 37-110) at any one point in time throughout the study.

Winter and summer survival of red squirrels was calculated from 27 years of population monitoring. Every squirrel in the population was followed from birth to death and censused every May and August. Mortality rate was calculated as the proportion of the population that was last seen or trapped by the project in a given census divided by the number of weeks between each census.

Red squirrel and snowshoe hare seasonal population dynamics

As part of the long-term Community Ecological Monitoring Project, twice a year (once in the spring prior to breeding and once in the autumn post breeding) we estimated the population density of snowshoe hares (and arctic ground squirrels and northern red-backed voles, see supplementary materials) through mark recapture trapping (see methods in (Krebs et al., 2001, 2014)). As part of the long-term Kluane Red Squirrel Project, all squirrels within a 72 ha section of the same study area are followed from birth to death, and population is censused twice a year in May and August providing exact densities (see McAdam et al., 2007). For hares and red squirrels (and, in supplementary materials, red-backed voles and ground squirrels), we calculated summer rate of increase as the proportional change in density between spring and autumn relative to the spring density. Winter rate of decrease was calculated as the proportional change in density between autumn and the following spring relative to the autumn density.

Global analysis of small mammal population dynamics

We calculated species-specific annual rates of increase and decrease, and population stability using all small mammal populations within the families *Rodentia, Lagomorpha,* and *Insectivora* for which there were at least 12 years of densities in the Global Population Dynamics Database (NERC Centre for Population Biology Imperial College, 1999). Since population cycles are known to vary between populations and we were interested in the potential ability of a species to cycle, we extracted the maximum measured annual rate of increase, decrease, and population CV for each species. Rates of increase and decrease were calculated at the proportional change in population densities between years.

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Chapter 6 - Summary and Conclusions

Discussion of general thesis results

Behaviour is often considered to be unpredictable with high variability due to the perceived complexity that goes into decision making and individual difference from personality. Although this may be true when trying to predict decisions at small scales like patch use, prey selection, and whether to move at this moment or the next, it is not true at longer time frames. I found that when the scale of interest is extended to the accumulation of decisions over a day, the predictability of behaviour across seasonal and multiannual timeframes becomes incredibly high since the variation over a year exceeds the individual variation within a day (see Chapter 4). By considering that activity patterns over seasons and years are predictable and species-specific, I also show that the level of flexibility in seasonal activity that a species has determines the rate of production and stability of population dynamics.

It may seem surprising that the simple theoretical foundations about activity that I produce here have not been previously assessed given the early interest within ecology in quantifying behaviour of animals. Activity patterns have always been one of the first aspects of a species' natural history to be characterized, in that for almost any species we know whether it is nocturnal, diurnal, crepuscular, etc. (Burkhardt, 1999). Despite this our ability to study behaviour in free-ranging species has been severely limited until recently. The classic studies all relied heavily on direct observations, which not only consumed considerable amounts of manpower and time for relatively small sample size, was restricted to species that were conducive to observation, and came with the biased outcome of the observer influencing the behaviour of the individual (Altmann, 1974; Altmann & Altmann, 2006; Crofoot et al., 2010). These restrictions placed a limit on the duration and number of individuals that could be observed and thus on the scales at which behaviour was studied. The theoretical advancements in our knowledge of behaviour that this thesis achieved (Chapters 4 and 5) were completely dependent on access to highly detailed and continuous behavioural data over long time frame made possible by biologging technologies for which a substantial part of this thesis was centered around (Chapters 2 and 3).

Although the biologging technologies that are the focus of the first half of the thesis are not new to biologists – having been used in marine studies for decades - their recent miniaturization has only recently allowed deployment on small animals, making them relatively new to terrestrial ecologists (Block, 2005; Rutz & Hays, 2009). Indeed, their inclusion in terrestrial wildlife studies has increased exponentially since the start of this thesis. This explosion has brought with it a desire to record behaviour for longer durations than can be achieved with the battery size restrictions imposed by small mammals. Chapters 2 and 3 show that this issue can be alleviated by reducing the recording frequency below the recommended Nyquist frequency (Williams et al., 2019) at the trade-off of classifying behaviour to broader categories than highlighted in the literature, and adjusting the classification methodology to account for this broader scale. Although at these long time scales it might not be possible to count stride frequencies or calculate speed of movement, it is possible to capture feeding or travelling bouts at the benefit of recording behaviour for weeks to months, instead of hours to days. Although detail is always thought to be better and more informative, the analysis done in Chapters 4 and 5 highlight that there is considerable value to studying behaviour in very simple, but ubiquitous forms. In these chapters, quantifying behaviour of an organism as active or inactive provided remarkable amounts of information about the species.

The high predictability of a bottom-up regulated bioenergetic model of activity (Chapter 4) raises questions about the role of predation risk to broad scale behaviour. Any search on the literature surrounding animal behaviour will highlight the recurring importance of predation risk to activity and foraging decisions (see Lima & Dill, 1990). However, our modelling of daily activity that only incorporated resource availability, temperature and mating opportunities produced predictions that matched seasonal and multiannual variation in daily activity with a surprisingly high correlation ($R^2 = 0.87$). Since most work done on animal behaviour is focused at decisions made over short time frames like timed trials in laboratories or patch selection for foraging, we currently know very little about how these observed effects manifest over longer time windows. It is possible that animals may compensate for reductions in activity during one moment by increasing activity at other times or places within the day. I showed an example of this type of compensation occurs in snowshoe hares in response to moonlight (Chapter 3). Although not in alignment with most theories it would make sense that if the choice is between not eating and certainly starving, or eating and only potentially being predated, that at a daily scale, activity should not be affected by predation risk. Alternatively, it is possible that variation in predation risk over time is highly correlated with temperature or resource availability and was thus was inadvertently captured in our model. Needless to say, the question of how predation risk influences daily activity is left as an important knowledge gap stemming from the work that I have done in this thesis that requires attention to advance our theoretical understanding of behaviour variation observed over seasons and years.

Integrating activity into bioenergetic consumer-resource dynamical equations generated predictions that seasonal flexibility of behaviour drives aspects of population dynamics. Although I found empirical support for most of these predictions, some remained partially untested. Through modelling I showed that species with inflexible seasonal behaviour are prone to larger rates of increase and decrease resulting in more unstable population dynamics than species with flexible seasonal behaviour (Chapter 5). Empirically I was able to show that this is potentially the case across small mammals, but did so through a reliance the extreme cases of hibernators and torpor users vs homeotherms. However, the rest of that chapter is centered around two homeotherms (red squirrels and snowshoe hares) with drastically different flexibility in activity. Outside of hibernation and torpor use (McLellan & McLellan, 2015), there is a surprising lack of data on seasonal activity patterns for most species. Given the potential importance that I found of seasonal activity to population dynamics and species interactions, this baseline information is critically needed and should be of high priority for most species. Beyond collecting this information for each species, Chapter 5 also suggests a need to study behavioural patterns of populations across a gradient of seasonality. The final analysis of this chapter created a prediction that population cycles should have greater amplitudes in less seasonal locations due to higher production in longer, warmer summers. Given cycles are generally shown to dampen in warmer locations, this prediction creates a seasonal paradox of enrichment. The explanation to this may still have to do with activity. The relationship between activity and resource availability shown in the bioenergetic model in Chapter 4, suggests that activity patterns should be quite variable across the range of a species distribution. Unfortunately, our tendency to study species at only one field site, and only publish data once per species, means that we have essentially no data on how daily activity varies over space and between climates. Thus, with this thesis I conclude with a call for a more concerted effort to be made to not only characterize seasonal activity of different species but also to investigate how activity varies between populations within each species. This thesis shows that this characterization of long term behaviour is important, but also that it can be done relatively simply, as although I started out characterizing behaviour into multiple detailed states (e.g. feeding, foraging, travelling, sleeping; Chapters 2 and 3), I concluded by exploring theoretical concepts of a more basic, but ubiquitous, form of behaviour (active and inactive; Chapters 4 and 5).

Final conclusion and summary

My thesis objective was to examine how the environment shapes an individuals' choice between activity and inactivity and what implications this choice has on a species' engagement with, and the dynamics of, other species with which it interacts. To achieve this, Chapter 2 and 3 tested and developed novel approaches to the use and analysis of biologging technologies on small mammals. By increasing the scale at which behaviour is classified from acceleration recordings, I showed that accelerometers can be effectively used at lower recording frequencies than the current standard in the literature. This ability to reduce the recording frequency results in increased longevity of devices, and provided the means needed to monitor behaviour over the time scales required of the thesis objective.

Throughout the thesis, I explored how environmental variation across a range of temporal scales influences and structures behaviour of individuals. This included confirming that red squirrels are strictly diurnal with strong seasonal activity patterns driven by primary production, temperature, and mating opportunities, in addition to interannual pulse resource fluctuations (Chapter 2 and 4). Snowshoe hares, on the other hand, are generally nocturnal and crepuscular, adjust timing of foraging in response to the monthly lunar cycle, and have seasonal activity patterns that are dampened in comparison to red squirrels (Chapter 3 and 5). Overall, environmental variation is a key driver in the bioenergetic decision to be active or inactive when calculated at the scale of a day and monitored over seasons and years (Chapter 4). This shows that behaviour, which is often considered noisy, is actually highly predicted and likely bottom-up regulated when considered over longer time scales than normally observed.

Finally, I found that environmentally-driven activity determines the level of trophic engagement of species with the environment and with other species in the system (Chapter 5). By incorporating activity into energy-explicit consumer-resource dynamical equations, I created predictions that seasonal flexibility in activity determines the rate of energy intake, expenditure, and loss to predation throughout the year. Over the course of a season or year, these rates accumulate to determine the population rates of increase and decrease, and contribute to population stability over time. This revealed that resource-driven seasonal inflexibility of activity has a tendency to drive large amplitudes in population cycles. The implications of this are that regardless of whether we consider a system to be top-down regulated or not, regulation will always be, at least, partly bottom-up through resource-driven activity mediation of species interactions (also suggested by White, 2013). Finally, this thesis highlights that seasonal processes are fundamentally coupled (Chapter 2, 4, and 5). Given what happens in winter influences what happens in summer, and vice versa, this finding reveals that it is important that we begin to study ecology across all season and not just during the “active” season. Until we do, we will be limited in our ability to push our theoretical understandings further than they currently are and we will continue to struggle to explain the patterns we observe within one season.

Supplementary Materials

Supplementary Materials for Chapter 2

7.2.1 Collar construction method

The accelerometer units that we used came unpackaged so that we could construct collars to meet the specifications needed for the small size of the red squirrels. Below are the steps that were taken to protect the accelerometers from claws and teeth of the squirrels as well as the elements. The circuit boards came coated with a protective layer such as plastidip which we then labelled externally (2). We then added a layer of seran wrap (3) and candle wax (4) to protect against moisture. On top of that we constructed a hard casing using a strip from an aluminum drinking can (5). This was formed into a round housing and held in place around the accelerometer with electrical tape (6). Two circular aluminum end pieces were fashioned from the same can and attached with duct tape (7). Care was taken to ensure that all devices were in the same orientation on the animal, so as the device was sealed in the protective housing, the orientation was marked on the housing (8).

We used zip ties for the band of the collar. To give reference to the circumference of the collar when attaching, we mark the zip ties at 9 cm and 10 cm prior to construction (9). These are used when collaring the animal to ensure that no collar is attached too tight. To protect the neck of the squirrel from the rough edge of the zip tie, we coat the zip tie in two lengths of 1/8" heat shrink where the accelerometer will not be placed (10). To attach the accelerometer to the zip tie, we first used a piece of electrical tape (11), then heat shrink. A trapezoidal piece of ¾" heat shrink was used where the short side is the length of the accelerometer and the long side is 1.5X the length of the accelerometer (12). This is centered over the collar band and accelerometer with the short side lying against the band (13). When shrunk with heat, the long side of the heat shrink will fold up and around the base of the accelerometer (14) ensuring that it is securely attached to the collar.

1. All components needed for collar

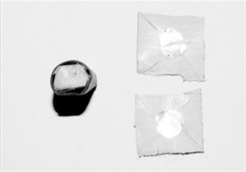
2. Labelled accelerometer.

3. Wrap in seran wrap.

4. Coat in layer of wax.

5. Cut aluminum strip as wide as unit is long.

6. Roll axy in aluminum strip and seal with tape.



7. Create aluminum protective ends.

8. Attach ends with tape. Label direction of axy.

9. Make collar band from ziptie.

10. Place band heat shrink where unit won't be.

11. Tape unit in place on collar band.

12. Cut 3/4" heatshrink in trapezoidal shape.

13. Place heatshrink over unit and collar band.

14. Shrink heatshrink to hold unit in place.

15. Completed accelerometer collar.

7.2.2 Red squirrel behavior data collection application

This application was designed and developed in 2014 to record instantaneous changes in behavior of wild red squirrels. This app was developed for IOS version 6.1.

The Application

The application consists of two screens: the first collects basic information about the individual that is being viewed and their initial behavior at first observation, the second allows the user to collect instantaneous behavior of the individual with a series of buttons. This saves all the data into 2 .csv files, one for each screen.

Screen 1:

OBS – Initials of the observer

Mode – Type of observation being made. On the red squirrel project, we distinguish between casual observations and schedule focal observations.

Colours – Identification markings of the individual. In red squirrels a unique combination of colored ear tags is used for identification.

Sex – Male or Female

Behaviour – a drop down list of behaviours appears to choose from including behaviours like feeding, travelling, and vocalizing.

Detail – for some behaviors there are additional details to be filled in. For example, if the animal is feeding, what is being consumed would be recorded in this variable.

Handedness – if the squirrel is feeding, we record whether it is using its left or right forepaw predominantly.

Time – time of observation. If button “Time” is pressed, the current time is filled in.

Loc X, Loc Y – the coordinates (X,Y) of the squirrel within the study grid.

Midden? – recorded whether or not the squirrel is on the center larder hoard within its territory.

Date – record the date of the observation. If button “Today” is pressed, the current date will be filled in automatically.

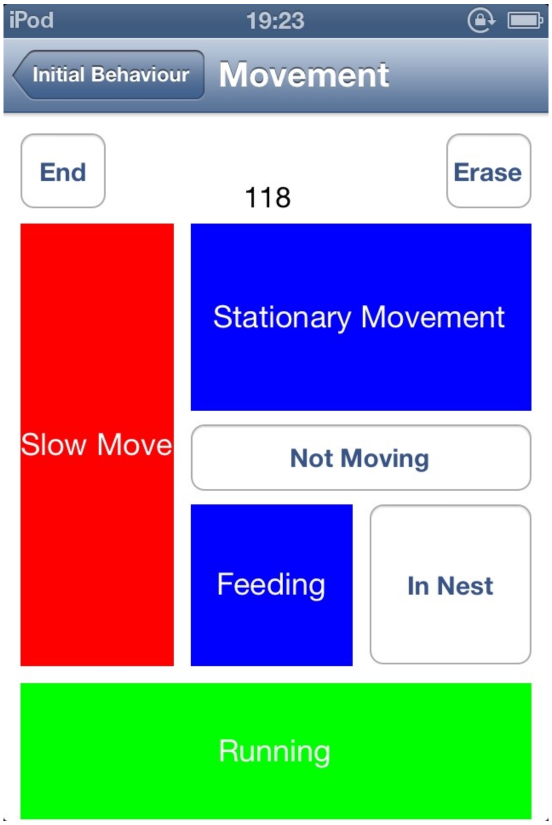
Comments – any additional comments can be recorded here.

Save – press this button to save the observation.

Next – press this button to proceed to the next screen without saving. Information from this screen such as observer, colours, and sex are transferred to the next screen and included in all data saved when on the next screen

Screen 2:

This screen collects instantaneous behaviour of the squirrel. It consists of 6 buttons that each represent a behavioral state. For the red squirrels, these behaviours included slow and fast travel (Slow Move, and Running), Stationary Movement (not moving in space, but body still moving including grooming and vocalizing), Not Moving, Feeding (actively consuming resources), and In Nest (not visible but telemetry signal triangulated to a squirrel nest).



Depending on the common duration of the behavior, the buttons had different functions when tapped. For behavioral states that tended to last longer than 10 secs at a time (Not Moving, In Nest, and Feeding), the application would record one line when the button is tapped indicating the start of the behavioral state. This requires that another button is pressed when the squirrel changes behavioral state to indicate the end of that state.

For behavioural states that typically occur at durations less than 10 seconds (Slow Move, Running, and Stationary Movement), two lines of data will be recorded when the button is pressed. The first when the button is pressed indicating the start of the behavior. The second when the button is released indicating the end of the behavior. For these behavioural states, user must press and hold the button for the duration of the behavior.

Additional functions of this screen include an “End” button that records a line of data indicating the end of the observational period. An “Erase” button that records a line indicating that the previous line of data was a mistake and should be deleted during post observation. There is a timer in the top center of the screen that counts down from 120 seconds to 0 indicating when to finish the observational period.

The Data

This application creates two data frames for different purposes. The first (table 1) creates a list of behavioral observations in the standard format used for the long term Kluane Red Squirrel Project. The second was the continuous observations used for this study. This data frame consisted of the observer, squirrel identification, sex, time, behavior, and whether it was when the behavior started or stopped, or the end of the observational period.

Table 1. Example of the data frame that is produced by screen 1 of the application.

id	obs	mode	lcolor	rcolor	sex	behavior	detail	hand	time	locx	locy	midden	date	com
13	EKS	adfoc	G!	P!	M	In nest			10:16:45	J.7	18.9	On	2014-02-19	
14	EKS	adfoc	R!	-	M	Travel	Tree		12:03:09	E.7	10.0	Off	2014-02-19	
15	EKS	adfoc	Y!	B!	M	Vigilant			12:14:42	C.3	13.1	Off	2014-02-19	
16	EKS	adfoc	W!	Y!	M	Vigilant			12:18:04	C.0	11.2	On	2014-02-19	
17	EKS	adfoc	B!	Y!	M	Feeding	Cone	R	12:26:21	J.2	9.6	On	2014-02-19	
18	EKS	adfoc	W!	O!	M	Vocal	rattle		12:34:12	J.7	6.6	Off	2014-02-19	
19	EKS	adfoc	O!	P!	M	feeding	mush		12:40:39	D.8	3.1	on	2014-02-19	

Table 2. Example of the data frame that is produced by screen 2 of the application.

ID	OBS	LCOLOUR	RCOLOUR	SEX	TIME	BEHAV	B2
49	EKS	Y!	B!	M	2014-03-20 11:03:17	Nest	PrStart
50	EKS	Y!	B!	M	2014-03-20 11:04:18	END	END
51	EKS	P!	W!	M	2014-03-20 11:24:20	Nest	PrStart

52	EKS	P!	W!	M	2014-03-20 11:25:22	END	End
53	EKS	W!	Y!	M	2014-03-20 11:35:15	StatMove	Start
54	EKS	W!	Y!	M	2014-03-20 11:35:21	StatMove	Stop
55	EKS	W!	Y!	M	2014-03-20 11:35:27	RunningMove	Start
56	EKS	W!	Y!	M	2014-03-20 11:35:37	RunningMove	Stop
57	EKS	W!	Y!	M	2014-03-20 11:35:59	StatMove	Start
58	EKS	W!	Y!	M	2014-03-20 11:36:00	StatMove	Stop
59	EKS	W!	Y!	M	2014-03-20 11:36:01	notmoving	PrStart
60	EKS	W!	Y!	M	2014-03-20 11:36:04	StatMove	Start
61	EKS	W!	Y!	M	2014-03-20 11:36:04	StatMove	Stop
62	EKS	W!	Y!	M	2014-03-20 11:36:05	Feed	Start
63	EKS	W!	Y!	M	2014-03-20 11:37:01	Feed	Stop
64	EKS	W!	Y!	M	2014-03-20 11:37:02	END	END

7.2.3 Time alignment

To align the clocks on the accelerometers with that on the behavioral observation, it was necessary to visually inspect the acceleration recording in and around the time of the observations to determine the extent of this mismatch. These time discrepancies appeared to be unique to each combination of squirrel, observer, and date. To determine the mismatch, we first identified in the behavioral observations clear transitions from substantial time (>10 sec) being spent not moving to moving as these transitions would generate a clear signal on the accelerometer. From this we were able to calculate the time mismatch for 47 and 13 observer squirrel days in the winter and autumn observation periods, respectively. Sample sizes were smaller in the autumn because at this time squirrels spent very little time not moving and large amounts of time running in comparison to the winter. Accordingly, we additionally identified in the autumnal data transitions from feeding (>30 sec) to fast travel (>7 sec) for additional calculations of time mismatch. From these additional transitions, we calculated the mismatch for a total of 39 observer squirrel days in the autumn. In total there were 11 observer squirrel days with multiple transitions on which a time mismatch could be calculated. In all cases the time mismatch tended to be within 2 seconds of the other transitions with the largest discrepancies being 8 seconds. In the situations where there was more than one transition, we used the mean time mismatch of all transitions for adjusting the time of the observations.

7.2.4 Temperature filtering

The temperature data loggers had a tendency to sporadically glitch throughout the recording. These glitches appeared to record a temperature that was considerably different (up to 10°C) from the 10 seconds before and after and would record the same temperature at each glitch. Thus, prior to any analysis, we filtered for these by determining the largest temperature difference that can occur naturally from one recording to the next, which is dependent on the temperature differential between in and out of the nest. Using temperature loggers (winter: n=10; autumn: n=10) that were visually confirmed to be functioning correctly over time, we calculated the maximum rate of temperature change from one recording to the next over 4 days (Table 1). Autumn recordings had a max rate of temperature change of -1.22°C and 1.10°C, and winter temperature differences maxed out at -4.40°C and 1.35°C. We identified any temperature recordings that had rates of change greater than 1.5°C per 10 seconds or 5°C per 10 seconds in autumn and winter, respectively. These temperature recordings were replaced by the mean temperature of the preceding and subsequent temperature recordings.

Table S7.2.1. Maximum temperature change between two temperature recordings on data loggers deployed on red squirrels in the winter (ambient temperature < 0°C) and autumn (ambient temperature > 0°C). This rate of change is influenced by the temperature differential between the nest and ambient temperature.

Accelerometer	MaxTempDiff (neg)	MaxTempDiff (pos)	Season
DD_Mar27_2014	-1.35	1.22	Winter
HH_Sep28_2014	-0.86	0.61	Autumn
TT_Sept24_2014	-0.86	0.86	Autumn
BB_Sep16_2014	-1.22	1.10	Autumn
NN_Sep28_2014	-1.1	0.98	Autumn
UU_Sept24_2013	-1.1	1.1	Autumn
ZZ_Sep28_2014	-1.22	1.1	Autumn
XX_Sept27_2014	-1.22	1.1	Autumn
AF_Sep29_2014	-1.22	0.98	Autumn
SS_Sep28_2014	-1.10	1.10	Autumn
DD_Sept25_2014	-1.1	0.86	Autumn
XX_Feb27_14	-1.83	1.22	Winter
OO_Mar2_14	-2.57	0.74	Winter
CC_mar4_2014	-4.4	1.22	Winter
YY_March4_2014	-2.81	0.98	Winter
II_Mar29_2014	-1.34	0.86	Winter
DD_Mar13_2014	-2.93	1.35	Winter
EE_Mar17_2014	-2.32	0.86	Winter
BB_Mar29_2014	-1.96	0.98	Winter
CC_mar4_2014	-4.4	1.22	Winter

7.2.5 Running means smoothing window for static acceleration

To separate static acceleration from dynamic acceleration, a running means smoothing window is applied to the raw acceleration. The smoothed file is the static acceleration. Dynamic acceleration is calculated by removing the static acceleration from the raw acceleration. Selection of the window size over which the smoothing function is important as too short a window may result in much of the dynamic acceleration being captured as static. This can cause implications on the summary statistics like ODBA that are derived from the dynamic acceleration. To determine if our selected window size (91 s) was appropriate we followed recommendations proposed by Shepard et al. (2008) and completed a sensitivity analysis by calculating ODBA using dynamic acceleration generated from running mean smoothing functions with windows ranging from 3 s to 220 s (Figure 1). For this we selected accelerometer files from 8 red squirrels and from each file we randomly selected one complete day of data producing 8 days of acceleration. As ODBA for different behavioral states may stabilize at different smoothing function window size (Shepard et al., 2008), we completed this sensitivity analysis for three different behavioral states: running (Figure 1a), foraging (Figure 1b), and feeding (Figure 1c). We confirmed that our window size (91s) was above the point at which ODBA became less variable with changes in the length of the running mean.

Shepard, E., Wilson, R., Halsey, L., Quintana, F., Gómez Laich, A., Gleiss, A., … Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology*, *4*(3), 235–241. doi:10.3354/ab00104

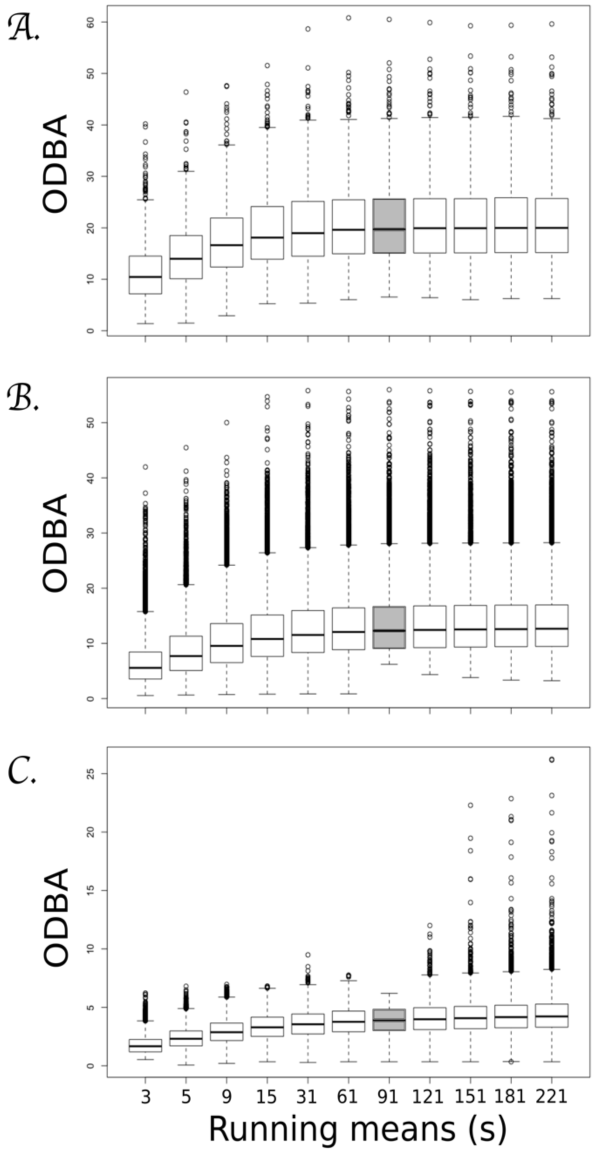


Figure S7.2.1. Change in overall dynamic body acceleration (ODBA; median and 25th/75th quantiles) as acceleration data is smoothed at increasing running means window sizes from 3 s to 221 s for running (A), foraging (B), and feeding (C) behavioral states over 1 day in 8 red squirrels. Grey box (91 s) represents the window size selected for calibration of red squirrel accelerometer data.

7.2.6 Video of squirrel behavioural states

Video can be found in the supplementary materials section at https://doi.org/10.1002/ece3.4786

Supplementary Materials for Chapter 3

Table S7.3.1. Summary of the number of observations of each behavior per hare per day recorded from six captive snowshoe hares for validating behavioral classification of accelerometer data.

Behavior	Min Num	Max Num	Mean Num	Mean Duration
Vigilance	2	150	42	10 sec
Sitting	1	46	9	45 sec
Sprinting	6	25	14	12 sec
Travel-multi hop	4	41	18	5 sec
Travel-one hop	4	58	13	5 sec
Feeding	1	26	8	30 ec

7.3.1 Smoothing window selection for removing static acceleration

Acceleration generated from the orientation of the device on the animal can be separated from behaviourally-derived acceleration by applying a running means smoothing window to the raw acceleration. Behaviorally-derived acceleration is then calculated by subtracting the long duration static acceleration from the raw acceleration. Selection of the window size over which the smoothing function is important as using too short a window may result in much of the behaviourally-derived acceleration being captured as static. To determine if our selected window size (91 s) was appropriate we followed recommendations proposed by Shepard et al. (2008) and completed a sensitivity analysis by calculating overall acceleration (OA) using the remaining acceleration generated from running mean smoothing functions with windows ranging from 3 s to 211 s (Figure S7.3.1). For this we selected 1 day of accelerometer data from each of the 6 captive snowshoe hare files. We confirmed that our window size (91s) was above the point at which OA became less variable with changes in the length of the running mean.

Shepard, E., Wilson, R., Halsey, L., Quintana, F., Gómez Laich, A., Gleiss, A., … Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. Aquatic Biology, 4(3), 235–241. doi:10.3354/ab00104

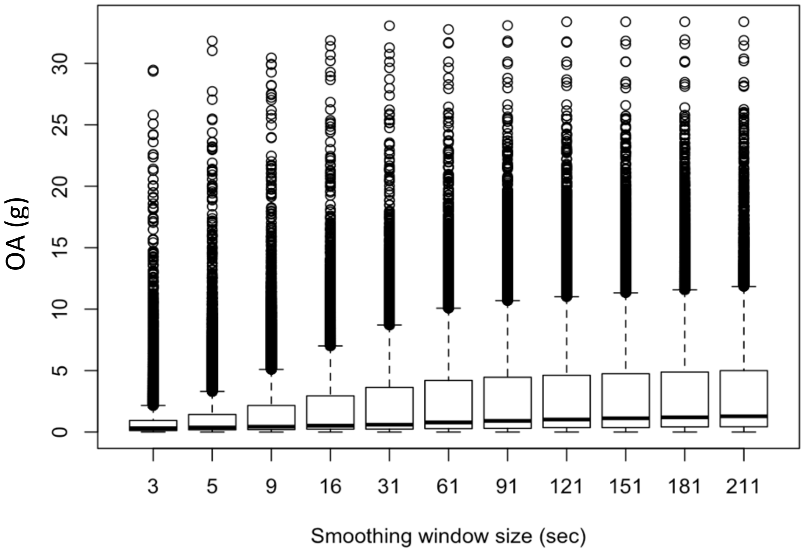


Figure S7.3.1 – Influence of smoothing window size for calculate of static acceleration on value of OA (g).

7.3.2 Random forest analysis for accelerometer classification

We distinguish all accelerometer recordings that were classified as moving into the 3 most common moving behaviours observed on snowshoe hares (vigilant, foraging, travelling; 95.2% of movement). We approached this using the random forest classification algorithm, which involves separating data into training and testing subsets. We used this algorithm to test how accuracy of classification varies with the sampling window of the accelerometer data. We tested 7 time windows (2, 4, 7, 10, 14, 20, and 30 seconds). For each window, we took the full data set of the continuous focal observations and separated it into segments of the desired time window, calculated the most common behaviours and the duration of those behaviours within that window. These observations were subsetted, selecting only segments that met the following criteria: 100% was not moving, 51% was travelling, or 51% feeding or foraging with 0% travelling. The proportion of observed data that met these requirements varied with the size of the time window with smaller time windows more likely to capture behaviour at the natural durations that is occurs (Table S7.3.1). Finally, we randomly sampled these to ensure that our dataset had equal numbers of each behaviour. Once the known behaviours were selected, we calculated 6 summary statistics on the dynamic acceleration of each axis including mean, standard deviation, maximum, sum, range, and sum of $\boxed{\Delta\alpha}$. We additionally calculated the overall acceleration (OA), ΔOA, min $\boxed{\Delta\alpha}$, max $\boxed{\Delta\alpha}$, max acceleration, mean pitch, and mean roll using all three axis together for a total of 25 different summary statistics. Using these statistics, we ran the random forest algorithm on a training subset (70% of data; growing 2000 trees) and calculated the % accuracy from the resulting confusion matrix on the testing data set.

Table S7.3.2. Percentage of observed snowshoe hare data that was included in random forest analysis at each time window after selecting segments that matched specific criteria.

Time Window (sec)	% Observed Data Used
2	95.2%
4	89.4%
7	78.5%
10	80.4%
14	75.9%
20	70.1%
30	61.7%

Results

The accuracy of the random forest increased with increasing time window from 83.3% at 2 seconds to 96.7% at 20 seconds (Figure S7.3.2). Above a sample window of 4 seconds, the accuracy of both not moving and travelling behaviour was consistently above 95%, while foraging was the most influenced by the sample window size increasing from 85.4% at 4 seconds to 93.0% at 30 seconds. However, this high accuracy at larger time windows comes at the trade-off of classifying behavior at durations that don’t naturally occur in snowshoe hares which will likely inflate the occurrence of short duration behavioural states (like travelling) while reducing the occurrence of long duration behaviour (like not moving).

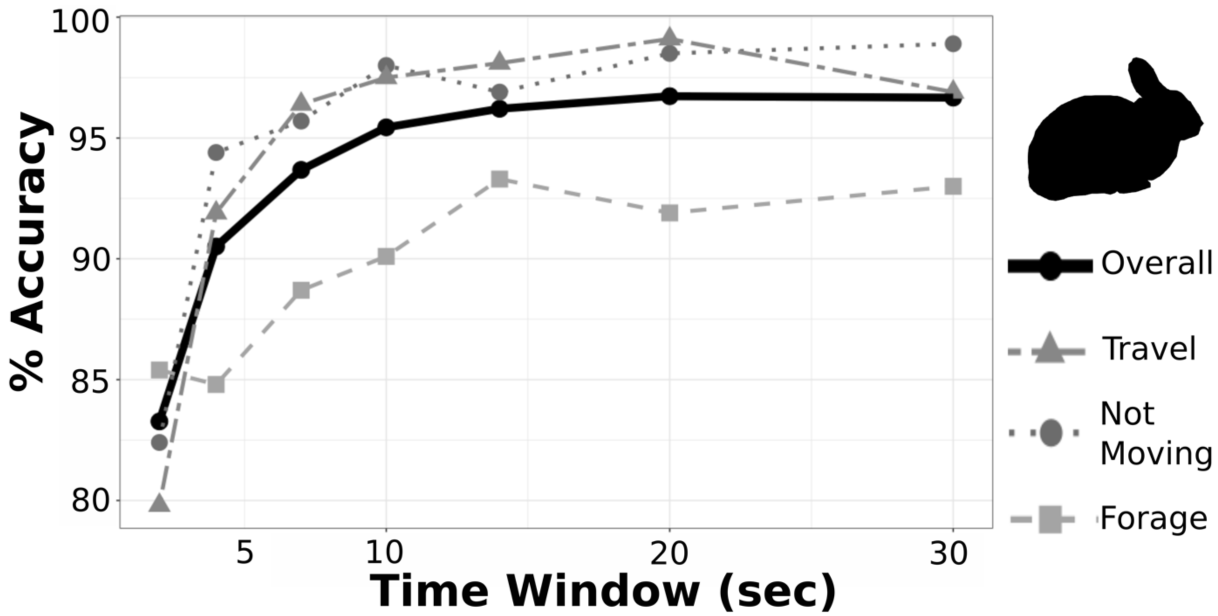


Figure S7.3.2 - Accuracy of random forest classification of snowshoe hare accelerometer data into behavior is influenced by the size of the time window over which acceleration summarized.

7.3.3 Recorder-specific acoustic classification analysis

Prior to any acoustic analysis we assessed the ability of independent listeners (n=3) to classify sounds to a behavior (Table S7.3.3). Acoustic properties of hopping, silence, and chewing sounds were initially measured for each recorder separately. Two recorders (hares B and C) had identical profiles for each sound, while one recorder had unique profiles for each sound (Figure S3). Thus, we combined all data from hares B and C for analysis and produced two sets of threshold values for automated classification of the three sounds (Table S7.3.4, S7.3.5).

Table S7.3.3. Inter-rater reliability at identifying chewing, silence, hopping, and unclassified sounds from acoustic recorders.

	Chewing	Silence	Hopping	Unclassified	Accuracy
Chewing	41	1	0	0	97.6%
Silence	0	40	1	1	95.2%
Hopping	0	0	15	13	55.6%
Unclassified	2	1	3	35	85.4%

Table S7.3.4. Upper and lower threshold values (dB) at each frequency used to identify silence, chewing, and hopping in 1 second audio clips for hare A.

	Silence		Chewing		Hopping	
Frequency	Lower	Upper	Lower	Upper	Lower	Upper
0	-1	13	4	14	8	40
0.25	-4.2	-0.08	-0.08	17.8	-0.08	26.5
0.6	-4.1	0.1	-3.1	5.9	-2.4	15.4
1	-5.7	-1.4	-5.7	0.1	-4.9	6.4
2	-9.4	-4.4	-9.1	1.4	-8.1	7.2
3.45	-11.7	-7	-11.8	-8	-8	5.9
6	-13.4	-8.1	-13.8	-8	-11.9	0.6
7	-12.7	-7.9	-12.5	-8.1	-11.8	-2.9

Table S7.3.5. Upper and lower threshold values (dB) at each frequency used to identify silence, chewing, and hopping in 1 second audio clips for hares B and C.

	Silence		**Chewing**		**Hopping**	
Frequency	Lower	Upper	Lower	Upper	Lower	Upper
0	2	13.1	4	22	4	41
0.2	-4.8	3.7	-2.2	20.3	-0.4	27.3
0.6	-4.7	2.3	2.3	28.2	4.1	33
1	-6.1	-1.6	-4.4	5.5	-4.5	18.5
2	-9.1	-4.4	-9	-3	-9.2	6.6
4	-13	-8.4	12.7	-7.5	-7.5	12
6	-13.8	-9	-13.7	-8.2	-12.4	-1.1
7	-13.1	-8.4	-12.4	-7.3	-12.6	-2.2

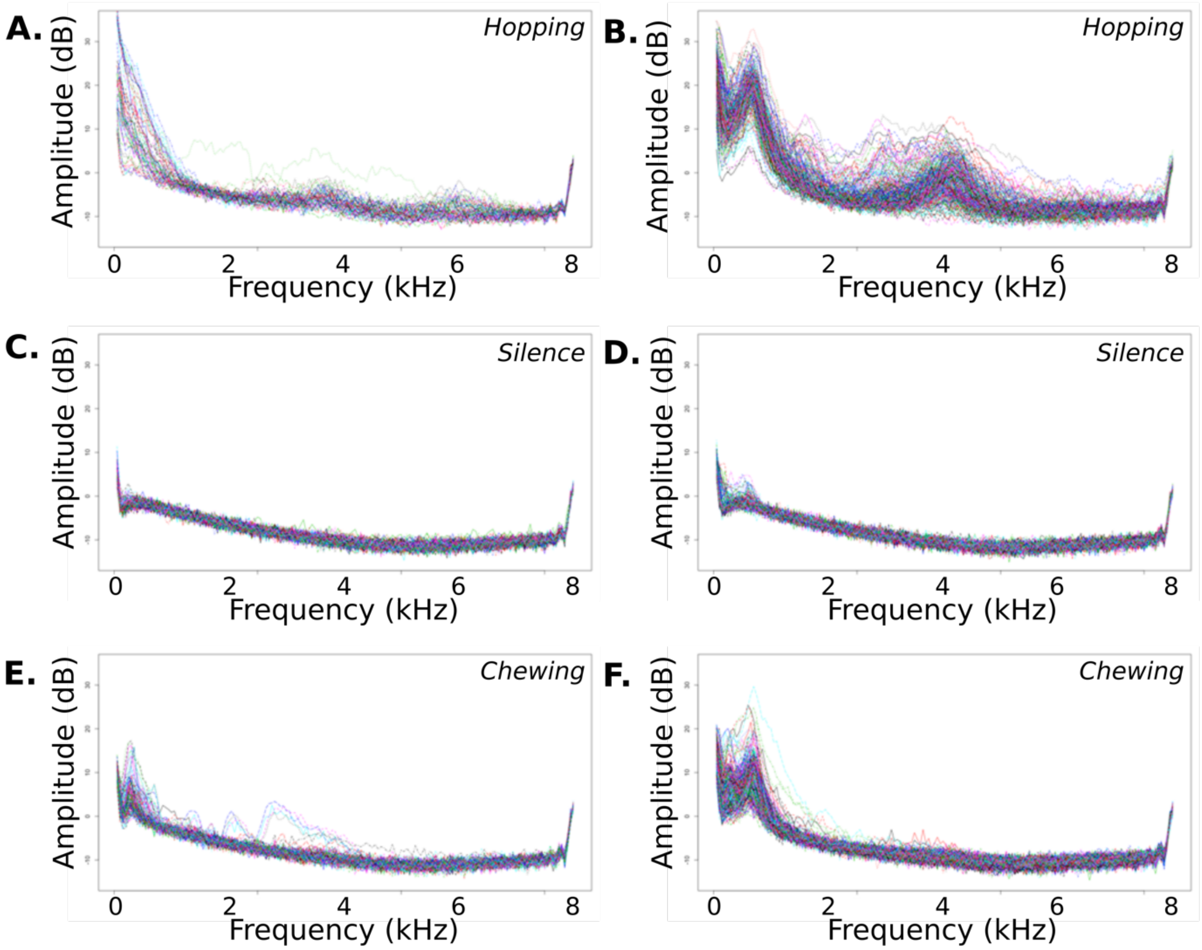


Figure S7.3.3 – Frequency-amplitude outputs of 1 second clips of animal-borne acoustic recordings on snowshoe hares (n=3) showing the sound profiles of hopping (A,B), silence (C,D), and chewing (E,F). Each line represents a different audio clip. Different recorders generated different profiles for the same type of sound. A,C, and E are sounds recorded from hare A, while B, D, and F are the same types of sounds recorded from hares B and C.

7.3.4 Individual accuracies of accelerometer behavioral classification for captive snowshoe hares

Table S7.3.6. Confusion matrix of classification of accelerometer data into three behavioral states for captive hare B2105. Overall accuracy was 85%.

	Not Moving	Forage	Travel	Accuracy
Not Moving	20	0	0	100%
Forage	1	15	4	75%
Travel	0	4	16	80%

Table S7.3.7. Confusion matrix of classification of accelerometer data into three behavioral states for captive hare B2729. Overall accuracy was 90%.

	Not Moving	Forage	Travel	Accuracy
Not Moving	19	1	0	95%
Forage	0	20	0	100%
Travel	0	5	15	75%

Table S7.3.8. Confusion matrix of classification of accelerometer data into three behavioral states for captive hare B2880. Overall accuracy was 91.7%.

	Not Moving	Forage	Travel	Accuracy
Not Moving	20	0	0	100%
Forage	2	17	1	85%
Travel	0	2	18	90%

Table S7.3.9. Confusion matrix of classification of accelerometer data into three behavioral states for captive hare B2891. Overall accuracy was 78.3%.

	Not Moving	Forage	Travel	Accuracy
Not Moving	19	1	0	95%
Forage	2	18	0	90%
Travel	0	10	10	50%

Table S7.3.10. Confusion matrix of classification of accelerometer data into three behavioral states for captive hare B2895. Overall accuracy was 76.7%.

	Not Moving	Forage	Travel	Accuracy
Not Moving	17	3	0	85%
Forage	3	16	1	80%
Travel	0	7	13	65%

7.3.5 Individual accuracy of acoustic behavioral classification

Table S7.3.11. Confusion matrix of acoustic behavioural classification for free-ranging snowshoe hare A. Overall accuracy is 92.2%

	Silence	Chew	Hop	Other	Accuracy
Silence	29	1	0	0	93.3%
Chew	0	27	1	2	90.0%
Hop	0	1	27	2	90.0%

Table S7.3.12. Confusion matrix of acoustic behavioural classification for free-ranging snowshoe hare B. Overall accuracy is 92.2%

	Silence	Chew	Hop	Other	Accuracy
Silence	29	1	0	0	96.7%
Chew	0	28	1	1	93.3%
Hop	0	4	26	0	86.7%

Table S7.3.13. Confusion matrix of acoustic behavioural classification for free-ranging snowshoe hare C. Overall accuracy is 97.8%

	Silence	Chew	Hop	Other	Accuracy
Silence	29	1	0	0	96.7%
Chew	0	29	0	1	96.7%
Hop	0	0	30	0	100.0%

7.3.6 Audio clips from acoustic recorders

Audio clips of not moving, forage, and travel can be found in the supplementary materials at https://www.frontiersin.org/articles/10.3389/fevo. 2019.00154/full#supplementary-material

Supplementary Materials for Chapter 4

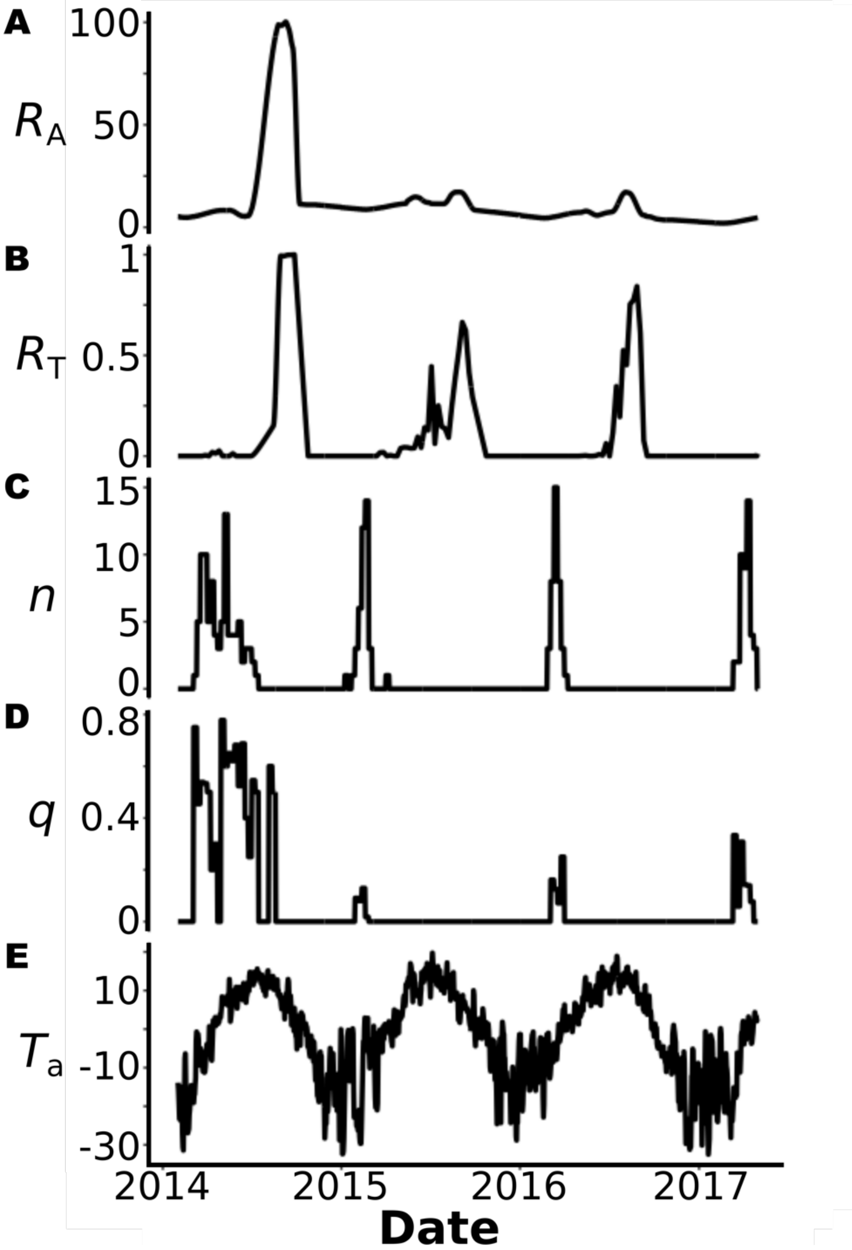


Figure *S7.4.1*. Measured and estimated temporal variation of Kluane abiotic and biotic variables relevant to red squirrel activity optimization including resource availability (R_a), proportion of available resources that are hoardable (R_t), number of mating events in a week (n), quality of offspring produced from mating event (q), and temperature (T_a).

7.4.1- Resource index, R_a

We assumed early autumn in mast years (when cones are mature, unopened, and readily accessible to squirrels; Archibald et al., 2012) represented maximum resource availability for this population and assigned a value of 100 to these periods to reflect 100% of maximum resource availability. Access to spruce cones at other times of the year, as well as access and use of other food resources were then scaled relative to this 100% maximum. Thus, our resource index is based on quantified production, hoarding, and consumption of spruce cones as well as feeding observations of alternative resources, and scales between 100 in the early autumn of a mast year to a possible minimum of 0 if squirrels completely lacked access to spruce cones and consumed no other alternative resources

Our resource index, R_{a}, is based on annual quantification of spruce cone production (cone counts), the number of cones hoarded by red squirrels (hoard-size sampling), and observations of the feeding behaviour of free-ranging red squirrels throughout the year (feeding observations). Our R index represents the contributions of various food types to squirrels across the annual cycle, including fresh cones, R_{aFC}, hoarded cones, R_{aHC}, spruce buds, R_{aB}, fungi, R_{aF}, and various summer pulse leaves, needles, and berries, R_{aP}, such that:

$$R_{\mathrm{a}} = R_{\mathrm{aFC}} + R_{\mathrm{aHC}} + R_{\mathrm{aB}} + R_{\mathrm{aF}} + R_{\mathrm{aP}} \qquad \text{(R1)}$$

R_{a} scales between 100 in the early autumn of a mast year to a possible minimum of 0 if squirrels completely lacked access to fresh (R_{aFC}) or hoarded spruce cones (R_{aHC}) and consumed no other alternative resources (R_{aB}, R_{aF}, or R_{aP}).

In this section, we explain the observations and assumptions involved in translating cone counts, hoard-size sampling, and feeding observations into estimates for each of these components, then conclude the section by describing how they were combined into a single index.

Fresh Cones, R_{aFC}

Prior to the hoarding season, fresh cones - still closed, maturing, and on spruce trees - are consumed by squirrels beginning in late spring or early summer. These fresh cones increase in energetic value and are consumed more as they mature over the course of summer, reaching a peak availability soon after the start of the hoarding season, when cone maturation is complete, cones have not yet begun to open (and disperse their seed), and few cones have been removed by squirrel hoarding activity. R_{aFC} is thus assumed to be 0 throughout winter and spring until feeding observations, for that given year, indicate squirrels have initiated fresh cone feeding. R_{aFC} is then assumed to increase in relation to i) increasing prevalence of fresh cone feeding in weekly feeding observations and ii) cone maturation, towards a maximum value at the start of the hoarding period. Every year in July prior to the beginning of spruce cone hoarding, we measured annual cone production by counting all cones in the top 1/3 of the tree visible from one direction for 586 trees in the study area. Total cones per tree was calculated using conversion generated by LaMontagne et al (2005; $\log(\text{actual total cones}) = 0.073 + 1.189 \times \log(\text{cone count})$). We refer to this annual measure as a cone count. Given the superabundance of cones on the landscape during mast years, we assumed that, at the start of the hoarding season in a mast year, $R_{aFCm} = 100$ (i.e., 100% of maximum), whereas in any other year, R_{aFCy} was $<< 100$, scaled according to the cone count in that year. Following its annual maximum, at the beginning of the hoarding season, R_{FC} was assumed to decline to 0 by the end of the hoarding season, due to squirrel hoarding activity (removing approximately 10% of cones) and cone opening and seed dispersal (all remaining cones). Because squirrel hoarding occurs throughout the hoarding season and accounts for only 10% of the reduction in R_{aFC}, whereas cone opening happens at the end of the hoarding season and accounts for 90% of the reduction, the decline in R_{aFC} from the start to the end of the hoarding season was assumed to be non-linear, remaining close to maximum values throughout most of the hoarding season, then marked by an accelerating towards 0 coincident with the end of the hoarding season.

Hoarded Cones, R_{aHC}

Red squirrels collect and hoard spruce cones during an autumn hoarding period in a larder hoard located at the center of individual food-based territories that they occupy and defend throughout the year. Hoarded cones are then consumed throughout winter and into the subsequent spring and summer. Every late September or early October, at the end of the hoarding season but prior to the ground freezing and snow accumulation, we quantified the total cones hoarded TC_{y}, averaged across 215 larder hoards (range: 187 – 236) sampled across two study grids as described in Fisher et al. (2019). Importantly, within this TC_{y} total, two types of cones can be and were differentiated in each larder hoard: 1) new cones hoarded during the current hoarding season, NC_{y}, and 2) old cones from previous autumn(s) still available in larder hoards, OC_{y}. We refer to this quantification of TC_{y}, including NC_{y} and OC_{y}, at the end of the hoarding season, as hoard-size sampling.

Annual consumption of hoarded cones, C_{HCannual}, between any two years, y and y+1 is:

$$C_{\mathrm{HCannual}} = (NC_{\mathrm{y}} + OC_{\mathrm{y}}) - OC_{\mathrm{y+1}} \qquad \text{(R2)}$$

Where NC_{y} and OC_{y} are the number of new and old cones that were present in autumn y and OC_{y+1} is the number of old cones present in middens in autumn y+1.

Consumption of hoarded cones is not evenly distributed across the year and varies primarily according to the availability and consumption of alternative resources. We used feeding observations of free-ranging red squirrels conducted throughout the year to quantify the proportion of observed feeding events that involved hoarded cones, p_{HC}, and grouped these observations into weekly estimates, $p_{\mathrm{HCw}1\text{-}52}$. If C_{HCw}, the number of hoarded cones consumed per week, varies proportionately with p_{HCw}, then:

$$C_{\mathrm{HCannual}} = \sum (C_{\mathrm{HCw}1:52}) = \sum \mathrm{x}\, p_{\mathrm{HC}1:52} \qquad \text{(R3)}$$

where x is a constant, reflecting the number of hoarded cones consumed in a week (for a given C_{HCannual}) when no other resources were consumed.

R_{aHC} was assumed, at the termination of hoarding period in year y, to reflect the total number of cones, TC_{y}, present in larder hoards including old and new cones (NCy + OCy). Following this, R_{aHC} was assumed to decline as a function of weekly cone consumption C_{HCw} over the course of the remainder of the winter, spring, and summer, until the start of the next hoarding period in y+1. Once autumn hoarding commenced, R_{aHC} was assumed to increase linearly from TC_{y} – sum $C_{\mathrm{w}1:48}$ at the start of the four-week hoarding period to TC_{y+1} at the end of the hoarding.

Mast cone production effectively swamps the hoarding capacity of red squirrels, meaning that only a fraction of cones available on the landscape are secured within squirrel larder hoards by the end of the hoarding season. The remainder open and their seeds wind disperse, rendering non-hoarded cones inaccessible to red squirrels following the hoarding season. In a mast year, squirrels can larder hoard approximately 10% of the cones available within their territories (Fletcher et al. 2013). Thus, we assumed a maximum value of 10 for R_{aHC}, occurring at the end of the hoarding season in the mast year, and scaled R_{HC} according to:

$$R_{\mathrm{aHC}} = 10\ (R_{\mathrm{HC\text{-}unscaled}}/TC_{\mathrm{m}}) \qquad \text{(R3)}$$

where $R_{\mathrm{aHC\text{-}unscaled}}$ is our estimate of average hoard size on a given day, and TC_{m} is the total number of cones in larder hoards at the end of the mast hoarding season.

Buds, R_{aB}

In late winter and early spring, red squirrels consume buds from spruce trees. The timing and extent of bud feeding by squirrels is well quantified by our feeding observations. As described in Fletcher et al. (2013), bud feeding commences in February, gradually increases through March and April, and peaks in May and early June when the vegetative and reproductive buds of white spruce end their dormancy and begin to rapidly grow and differentiate. We know little about the energy and protein returns achieved during bud feeding, but can use feeding observations to assess the extent to which squirrels prioritize feeding on buds versus hoard cones in later winter (across $\mathrm{R_{HC}}$ due to variable cone production and hoard size variation) and buds versus pulse resources in early summer. Accordingly, R_{aB}, was assumed to follow the seasonal prevalence of bud consumption in feeding observations (Fletcher et al. 2013), initiating in February, peaking in May and early June, and declining to 0 by early July, then remaining at 0 for the remainder of the year until recommencing the following February. We assumed the value and timing of annual maximum, and the timing of decline and summer termination were proportional to the prevalence of buds in weekly feeding observations. Initiation date (Feb 15) was held constant across all years due to limited inter-annual observations in February.

Fungi, R_{aFF} and R_{aHF}

Red squirrels feed on various fungi, including numerous unidentified mushroom species and hypogeous fungi-like truffles. These fresh food sources are available to squirrels from late spring to late autumn, during snow free periods when the ground is not frozen. In addition, red squirrels also hoard mushrooms and truffles, generally securing them in tree branches, where they dry and remain accessible for consumption during winter and spring periods of snow cover. Thus, within our feeding observations, mushrooms and truffles consumed during the growing season are almost always fresh fungi, R_{aFF}, whereas those consumed during periods of snow cover always involve hoarded fungi, R_{aHF}. We assumed squirrels consume fresh fungi when they are available on the landscape and set the onset, peak, and end dates of annual availability according to timing of initial, peak, and final presence in feeding observations, respectively. R_{aFF} was assumed to be zero outside of these dates and to increase from onset to peak and decrease from peak to end according to a parabolic curve. We did not quantify amount of hoarded fungi each year nor do we have feeding observations throughout the winter when consumption of R_{HF} would be at the highest. As such, we estimated R_{HF} throughout the winter as the proportion of feeding observation on hoarded fungi relative to hoarded cones during late February and early March each year. For example if feeding observations were 0.2 hoarded fungi and 0.8 hoard cones, than R_{aHF} for that winter would be 0.25 (0.2/0.8) the value of R_{aHC}.

Summer pulse leaves, needles, and berries, $R_{\text{a}P}$

Squirrels feed on leaves, needles, berries, and deciduous buds from various plant spp. that grow during the summer pulse. These plants begin to grow once the snow has melted with each food source likely reaching peak availability at different points throughout the summer. We used daily on-site snow depth measurements and field observations and weekly NDVI values for the area to estimate R_{aP} each year. We assumed summer pulse availability began when 90% of the study area became snow free, and ended at first permanent snow fall of the winter. The relative value of R_{aP} throughout the pulse was set according to NDVI scaling so that zero was equivalent to an NDVI value of 0.5. Any NDVI values below 0.5 during the snow-free period were removed and interpolation was used to estimate any missing values, ensuring that R_{aP} was above 0 throughout the pulse period.

To generate one resource variable, we scaled each variable relative to R_{FC} according to known information so that are R_a ranges from 0 to 1. R_{aHC} was scaled so that peak availability in the mast year (2014) was 10% peak R_{aFC} of that year, the average proportion of available cones that squirrels hoard in a mast year (Fletcher et al., 2010). The scaling of R_{aFF}, R_{aB}, and R_{aP} was set according to the equivalent cone index that would generate a similar maximum proportion of the diet. For example, fresh cone availability of 10% mast conditions generates a squirrel diet composition of 60% fresh cones. Peak consumption of fresh fungi was 60% of diet, thus we scaled R_{aFF} so that peak values equalled 0.1. R_{aB} and R_{aP} both had peak consumptions of 25% of diet, and were thus scaled so that peak values equalled 0.05. Our R_{aHF} estimate was calculated after R_{aHC} had been scaled and thus needed no further adjustments. Once scaled all components of resources availability were combined to generate a timeseries of R_a over the course of the study (Figure S1).

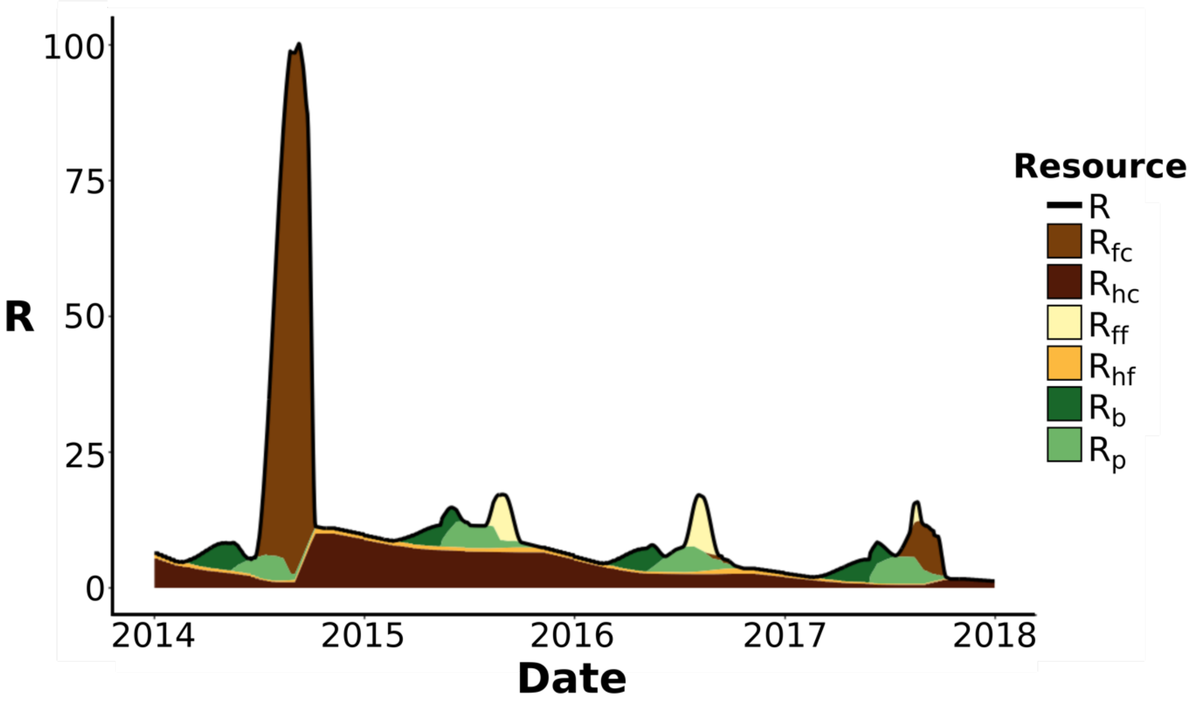


Figure S7.4.2. Relative resource availability (R_a) over the duration of the study is composed of seasonal and multiannual pulses of different resource types. Primary resources for red squirrels include fresh spruce cones (R_{fc}), hoarded cones (R_{hc}), fresh fungi (R_{ff}), hoarded fungi (R_{hf}), spruce buds (R_b), and summer pulse items (berries, leaves, needles; R_p).

7.4.2 – Resource type index (R_T)

Our index of resource type, R_t, as a proportion of available resources is 0 when all available resources are only consumable and 1 when all available resources are hoardable. Based on the seasonal extent of squirrel hoarding activities, generally R_t is 0 throughout winter and spring when no resources are hoardable, begins to increase in summer with the onset of fresh fungi availability, accelerates in late July or early August if fresh cones become available, then declines as hoarding declines. We estimated R_t from feeding observations (n = 22,513) of free-ranging squirrels in the study area that were recorded daily between March and October each year. For each week, we calculated the proportion of feeding events (average weekly observations = 132, range = 1-1290) that were on hoardable and non-hoardable resources. Since cone hoarding occurs only once cones mature but feeding occurs on all cone developmental stages, we restricted cone-influenced R_t to a maximum value of 0.1 prior to August 10 (onset of hoarding; Archibald et al., 2012), and interpolated values between the onset of cone feeding and this date, and this date and peak R_t. We further assumed that squirrels in winter (mid-October – end of January) had no access to new hoardable resources and, therefore, solely consumed previously stored food (R_t =0). For any remaining weeks with no feeding observations (n=9; 4%), R_t was interpolated assuming linearity between weeks (Figure S1).

7.4.3 - Modelling activity

Temperature-dependency of energy expenditure

Equation 5 states that *E* varies with air temperature (T_a); expenditure increases linearly per unit decrease of T_a below the lower critical temperature (T_{LC}) according to the Scholander-Irving thermoregulatory response. However, when temperature is above the T_{LC} and below the upper critical temperature (T_{UC}), *E* is independent of temperature such that:

$$E = C(T_b - T_a) \qquad \text{when } T_a < T_{LC}$$

$$E = M_{RMR} \qquad \text{when } T_{UC} > T_a > T_{LC} \qquad \text{(S1)}$$

where *C* is the rate of increase in expenditure per unit decrease in T_a, T_b is the body temperature, and M_{RMR} is the resting metabolic rate.

Inactive net energy gain

Combining equations 3 and 5b provides us with a model of net energy gain when inactive. The later equation states that expenditure when inactive is a function of temperature and refuge quality. Inactive individuals have the opportunity to use thermal refuges to reduce the rate of increase in energy expenditure when temperatures decrease. The rate of increase in expenditure when inactive (C_i) is dependent on the extent of refuge quality (*Q*) and the rate of increase in expenditure per unit decrease in T_a when no refuge (C_a) is used such that:

$$C_i = C_a - C_a Q \qquad \text{(S2)}$$

where *Q* ranges from 0, when there is no thermal refuge, to 1 when the thermal refuge maintains temperature within the thermoneutral zone. By substituting equations S1 and S2 into 3, energetic gain of inactivity incorporating thermal refuge use can be represented as:

$$G_{EI} = -(C_a - C_a Q)(T_b - T_a) - C_a Q(T_b - T_{LC}) \qquad \text{when } T_a < T_{LC}$$

$$G_{EI} = - M_{\mathrm{RMR}} \qquad \text{when } T_{\mathrm{UC}} > T_{\mathrm{a}} > T_{\mathrm{LC}} \quad \text{(S3)}$$

Active net energy gain

By substituting equation S1 into 4 we can model net energy gain of activity as:

$$G_{EA} = I - AC_{\mathrm{a}}(T_{\mathrm{b}} - T_{\mathrm{a}}) \qquad \text{when } T_{\mathrm{a}} < T_{\mathrm{LC}}$$

$$G_{EA} = I - A^{*}M_{\mathrm{RMR}} \qquad \text{when } T_{\mathrm{UC}} > T_{\mathrm{a}} > T_{\mathrm{LC}} \quad \text{(S4)}$$

If consumption is on only resource type, then the diminishing returns over time of that resource will influence I according to equation 6. However, not all resources will have equal diminishing returns. If we assume that an individual's diet is composed of two types of resources (i and j), then equation 6 is modified to be:

$$I_{(t)} = R_{ti}R_{\mathrm{a}}/\alpha_{\mathrm{i}}^{\mathrm{t-1}} + (1 - R_{ti})R_{\mathrm{a}}/\alpha_{\mathrm{j}}^{\mathrm{t-1}} \qquad \text{(S5)}$$

where R_{ti} is the proportion of available resources that are resource type i, α_{i} defines the diminishing returns of resource i, and α_{j} defines the diminishing returns of resource j.

Net reproductive gain

Net reproductive gain is represented in equation 7. As this gain was not time explicit we modelled G_{R} at each time interval as a discrete random variable with a probability space of two outcomes: 1 if individual should be active and 0 if individual should be inactive according to:

$$P(G_R = 1) = nqm \qquad (S6)$$

Table S7.4.1. Definition of variables, units, and parameters present on our model of activity. Values of constants used in simulations of the model are provided along with reference from which value was extracted.

Variable	Subvariable	Definition	Unit	Value used in simulations
G	G_{Ei}	Net energy gain of inactivity	W	calculated
	G_{EA}	Net energy gain of activity	W	
	G_R	Net reproductive gain		
I		Energy Intake	W	calculated
E	E_i	Energy expenditure inactivity	W	calculated
	E_a	Energy expenditure of activity	W	
A		Activity multiplier equal to the factor that expenditure is increased above inactivity		2; assumed to double when active (Karasov, 1992)
T	T_a	Ambient temperature	°C	-30°C to 20°C by 0.5°C increments
	T_b	Body temperature	°C	38°C (red squirrel) (Pauls, 1979; Humphries & Umbanhowar, 2007)
	T_{LC}	Lower critical temperature defining lower boundary of thermoneutral zone.	°C	15°C (red squirrel) (Pauls, 1981)
M_{RMR}		Resting metabolic rate.	W	1.215 W (red squirrel) (Pauls, 1981)
C	C_a	Conductance; rate of increase in expenditure per unit decrease in T_a for activity.	W	Ca = 0.05325 W (red squirrel); (Pauls, 1981)
	C_i	Conductance; rate of increase in expenditure per unit decrease in T_a for inactivity.	W	Ci was calculated using eq. S2
Q		Refuge quality		0.5 (red squirrel) (Guillemette et al., 2009)
R	R_a	Resource availability index; sum of multiple resource types		5 (low), 20 (moderate), 60 (high)

	R_t	Proportion of available resources that are of a particular type (hoardable vs non-hoardable)		$R_{ti} + R_{tj} = 1$; $R_{ti} = 0$, 0.5, 1
α		Diminishing returns coefficient representing satiation. Varies with resource availability and type		$\alpha_{\mathrm{i}} = 1.02$; $\alpha_{\mathrm{ii}} = 1.04, 1.06, 1.08$ *with low, moderate, and high resources, respectively*
n		number of potential mating events		*
q		quality of offspring produced by mating		*
m		mating conversion factor equal to the rate at which activity is expected to increase per unit of nq		0.05

* for simulations, a combined n and q variable was used that ranged from 0 to 12 at increments of 1. We did not assess each variable on its own. The geometry of a population cycle: a mechanistic model of snowshoe hare demography

7.4.4 – Fitting diminishing returns to modelled activity

We assessed how the accuracy of the model at predicting observed activity of red squirrels varied as we adjusted the diminishing return values of the resources. Rates of diminishing returns likely increase with resource availability as individuals become satiated more quickly. Assuming this relationship is linear, we assessed all combinations of minimum and maximum $\alpha_{\mathrm{Hoardable}}$ and $\alpha_{\mathrm{Non\text{-}hoardable}}$ values at 0.01 increments between 1.0 and 1.4. For the combination of $\alpha_{\mathrm{Hoardable}}$ and $\alpha_{\mathrm{Non\text{-}hoardable}}$ values that generated the highest accuracy we calculated Pearson's R correlation between predicted and observed values as a secondary measure of fit.

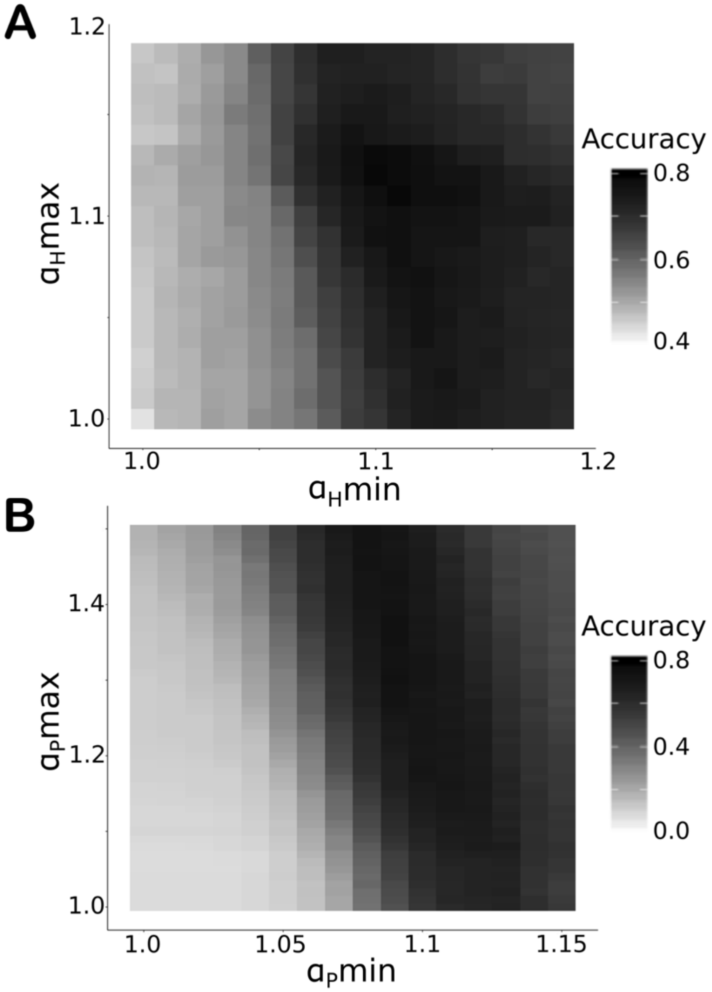


Figure S7.4.3. Assessment of model accuracy in relation to diminishing returns values for hoardable (α_H, top) and non-hoardable (α_P, bottom) resources. Model allows diminishing returns values for both hoardable and non-hoardable resources to vary linearly with resource availability such that min values are applied to lowest observed resource values and max values are applied to the highest observed resource values.

7.4.5 – Measured activity model results

Table S7.4.2. Model selection table for the proportion of 24 hours spent active by red squirrels including the log likelihood, AIC value, delta AIC, and model weight of each model. Explanatory variables included in each model are represented by a ‘Y’. Explanatory variables are resource availability (R_A), proportion of available resources that are hoardable (R_T), temperature (T_a), reproductive status (B), reproductive opportunities (nq), and interaction terms between these single variables.

Model	R_A	R_T	T_a	B	nq	R_A:B	R_A:nq	R_A: R_T	R_A: R_T: T_a	df	LogLik	AIC	deltaAIC	weight
1	Y	Y	Y	Y	Y	Y	Y	Y	Y	19	-50090	100217	0	1
2	Y	Y	Y	Y	Y			Y	Y	15	-50109	100248	31	0
3	Y	Y	Y	Y	Y	Y	Y	Y		16	-50246	100523	306	0
4	Y	Y	Y	Y	Y			Y		12	-50269	100561	344	0
5	Y	Y	Y	Y	Y	Y				14	-50274	100576	359	0
6	Y	Y	Y	Y	Y	Y	Y			15	-50273	100577	360	0
7	Y	Y	Y	Y	Y		Y			12	-50288	100601	384	0
8	Y	Y	Y	Y	Y					11	-50290	100602	385	0
9	Y									5	-50602	101214	997	0
10		Y								5	-50771	101552	1335	0
11			Y							5	-50808	101626	1409	0
12				Y						7	-50962	101938	1721	0
13					Y					4	-50986	101972	1755	0

Supplementary Materials for Chapter 5

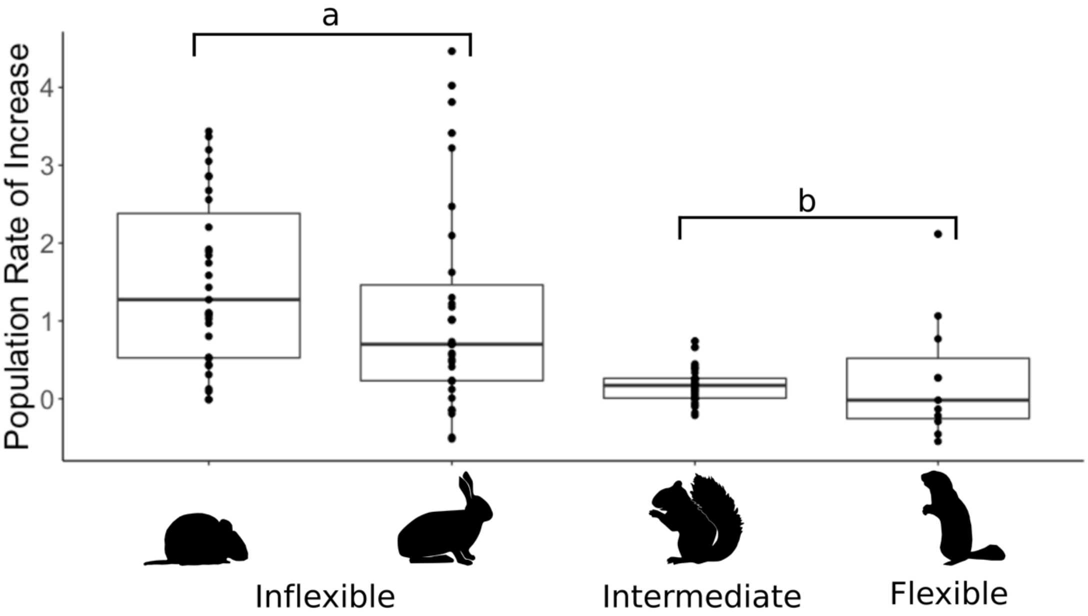


Figure S7.5.1 – Summer population rates of increase of small mammal populations in Kluane, Yukon observed over 30 years. Behaviourally inflexible species (red-backed vole and snowshoe hare) have, on average, greater population increases than behaviourally flexible species (red squirrel and arctic ground squirrels). Letters denote significant differences ($p<0.001$) in population rates of increases between species.

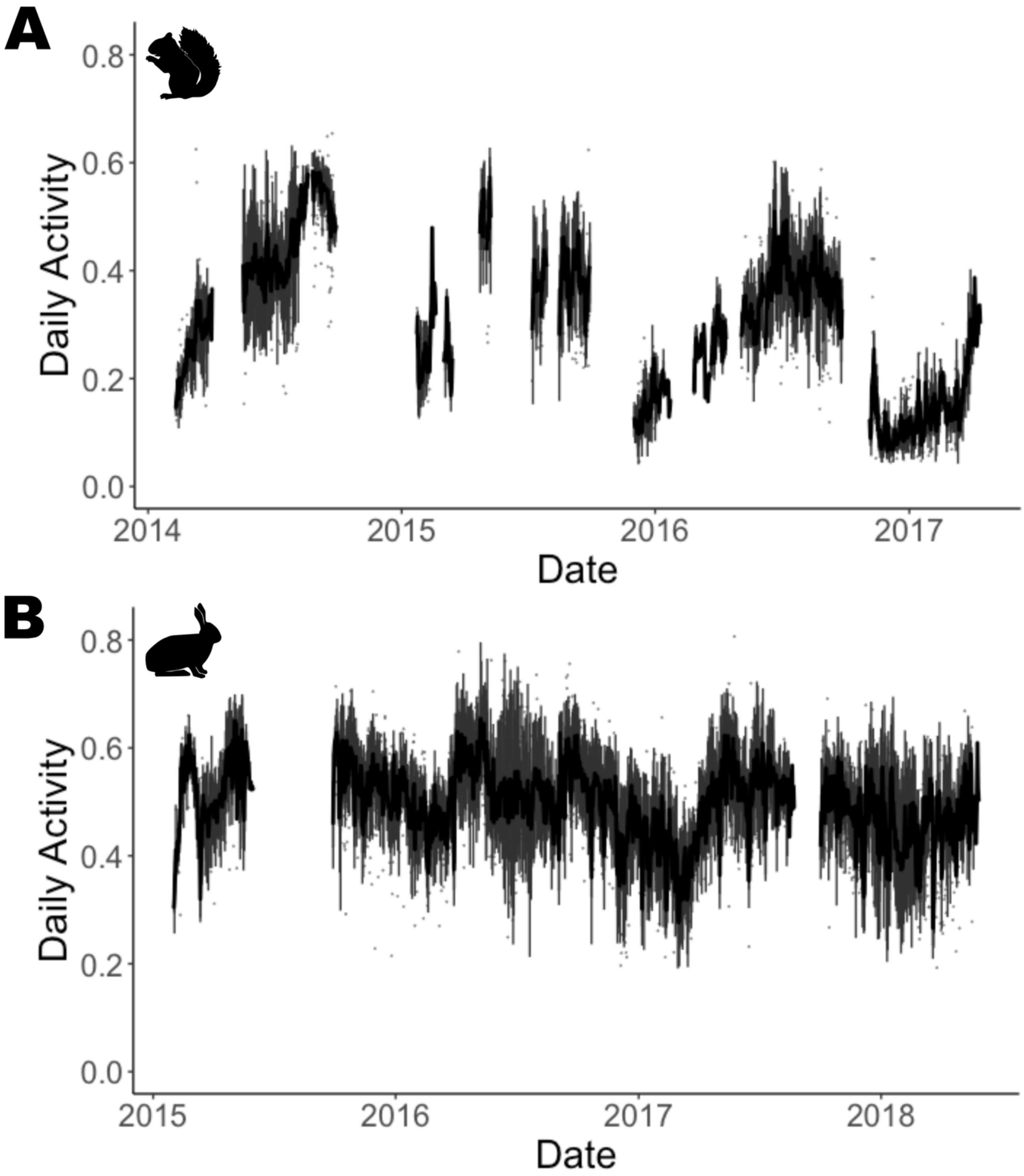


Figure S7.5.2 – Daily activity values recorded using accelerometers on red squirrels (a; n = 489) and snowshoe hares (b; n = 279) over four years.

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