







LETTER

Optimisation of energetic and reproductive gains explains behavioural responses to environmental variation across seasons and years

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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 optimisation of the relative energetic and reproductive gains each state offers. We show that this simplified behavioural decision approach predicts most activity variation ($R^2 = 0.83$) expressed by free-ranging red squirrels over 4 years, as quantified through accelerometer recordings (489 deployments; 5066 squirrel-days). Recognising 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 optimisation of gain, provides an integrated approach to examine behavioural variation as an intermediary between environmental variation and energetic, life-history and ecological outcomes.

Keywords

Accelerometer, behaviour, decision-making, energetic gain, hoarding, metabolic ecology, optimal behaviour, *Tamiasciurus hudsonicus*.

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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 characterise behavioural responses in a generalised, 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, Boudreau, *et al.*, 2019). Accordingly, we focus the next two paragraphs on describing an empirical approach for categorising behavioural variation and a conceptual approach to relating these behavioural categories to their energetic and ecological consequences.

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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) minimises 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 generalisable 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, Hock, Walters, & Irving, 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 modelled 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 & Dingemans, 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 optimisations 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 hypothesised that behavioural responses to seasonal and multiannual variation in resources, temperature and mating are optimised 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. This 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 h), 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 modelled 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 Klune 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, Landry-Cuerrier, *et al.*, 2019 for collar design). All accelerometers recorded acceleration between $\pm 8 g_{\text{forces}}$ 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, Boudreau, *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 were 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, Landry-Cuerrier, *et al.* (2019). Briefly, animals were nesting 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 $1.06 g_{\text{forces}}$. 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 h 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 categorising 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 normalised difference vegetation index values extracted for the study area from MODIS (winter: $\text{NDVI} < 0.35$, spring: $0.35 < \text{NDVI} < 0.61$ and day of year < 200 , summer: $\text{NDVI} > 0.61$, autumn: $\text{NDVI} < 0.61$ and day of year > 200 ; Didan, 2015). Following this analysis, we tested whether activity between sunrise and sunset (represented as proportion of 24 h) 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 generalised 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 optimisation model to assess how, in theory, daily activity should respond to variation in temperature, resources, and mating opportunities if animals optimise inactive and active states. A basic version of this model is described in Humphries and Umbanhowe (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 modelling 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 maximises net energy gain (G_e) and net reproductive gain (G_r) such that:

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

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:

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

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 characterised by $I = 0$, such that

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

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

$$G_{ea} = I - AE_i \quad (4)$$

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

$$E = f(T_a) \quad (5)$$

where T_a is air temperature and the function, f , assumes a Scholander–Irving thermoregulatory response (Scholander, Hock, Walters, & Johnson, 1950). Given the potential that thermoregulatory costs can be reduced by occupying a thermal refuge when inactive, then

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

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

where Q is the 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 the 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 the following:

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

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 the 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 ,

$$G_r = nqm \quad (7)$$

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 eqns 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 and 2.4 h 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 min 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 ($F = 505$, d.f. = 9, $P < 0.001$; Fig. 1a–d). Squirrels were most active in autumn, averaging 75.2% of daylight hours (10.1 h), and least active in winter, averaging 43.1% of daylight hours (3.73 h). Activity during the night averaged 2% (9 min; range 0–70 min) with little variation between seasons. Dawn and dusk activity was generally limited (*c.* 5 min per period) except during autumn when activity would begin during the dawn period (*c.* 16 min per period).

Red squirrel activity varied seasonally and multi-annually, with individual values ranging from 1 to 15.5 h 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 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

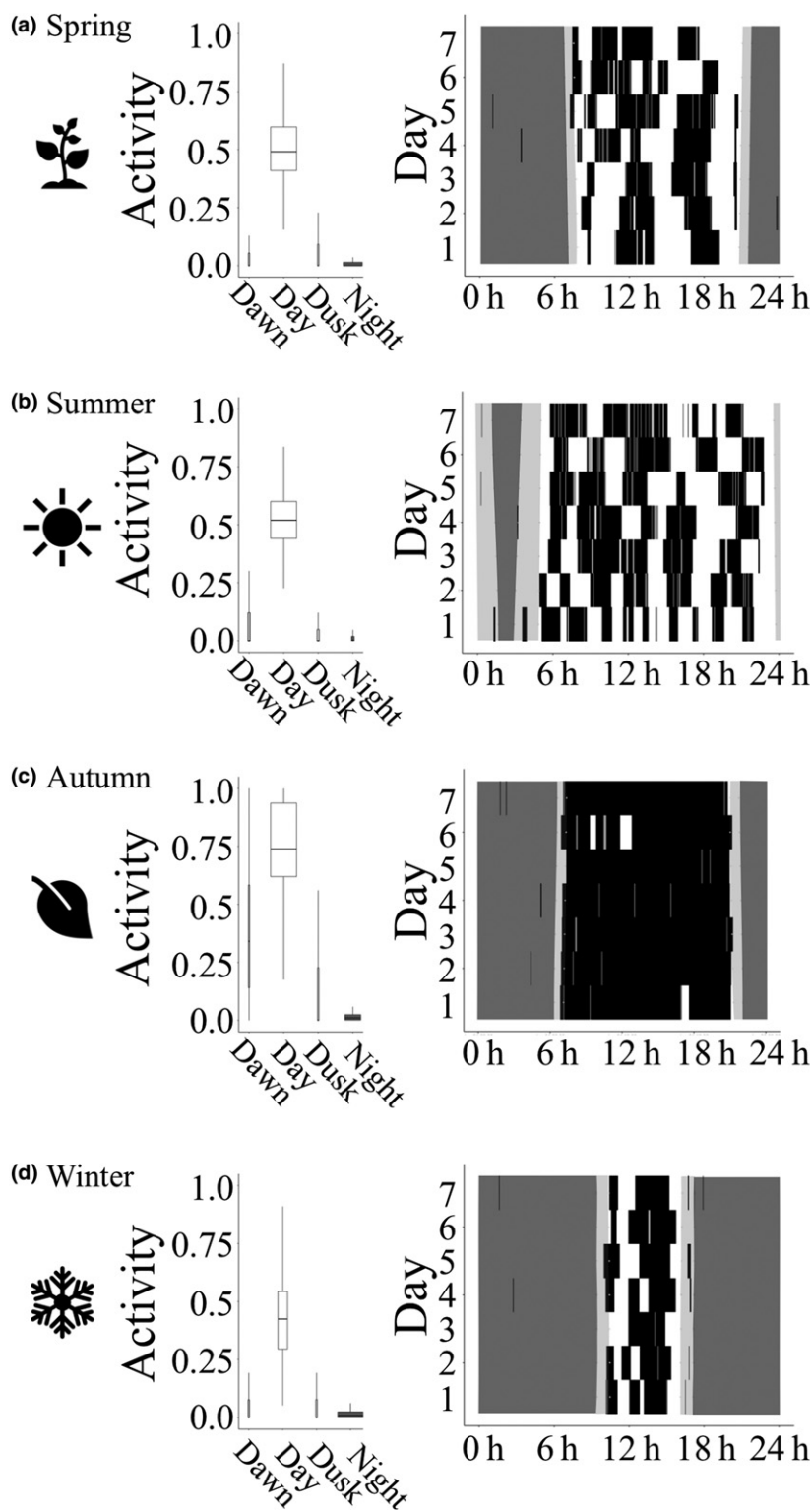


Figure 1 Seasonal variation in observed red squirrel ($n = 225$) activity and inactivity throughout the day recorded using accelerometers. The timing and amount of activity varies according to each season (spring (a), summer (b), autumn (c) and winter (d)). Timing of daily activity is presented as proportion 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.

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 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; $z = -0.25$, $P > 0.05$).

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 ($\alpha_{\text{Hoardable}} = 1.10\text{--}1.12$, $\alpha_{\text{Non-hoardable}} = 1.09\text{--}1.35$) predicted squirrel activity within 1.2 h of the observed daily mean 59.8% of the time and within 2.4 h 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). 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 h 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).

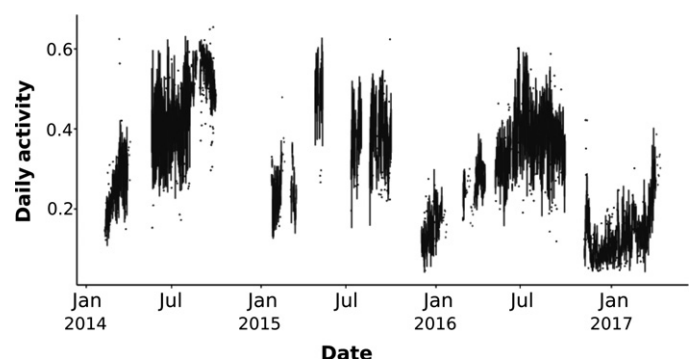


Figure 2 Observed daily activity (proportion of 24 h) of free ranging red squirrels ($n = 225$) recorded using accelerometers over three and half years. Each date is represented as a boxplot denoting the 25 and 75 quantiles with dots representing activity outside that range.

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 availability and quality, air temperature and presence of mating opportunities. Our analyses suggest that activity reflects an optimisation of energetic and reproductive gain, with individuals active when the gains of activity outweigh the gains (or minimisation 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 optimisation 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 categorisation 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 optimisation (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

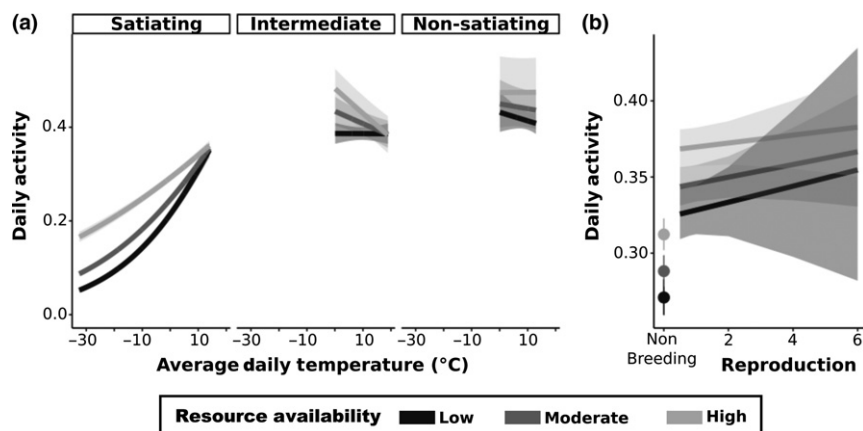


Figure 3 Daily activity (proportion of 24 h) responses to temperature, resources, and reproductive opportunities. The effects of temperature on activity were dependent on resource availability and resource type (a), while the effects of mating opportunities were dependent on resource availability (b). 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).

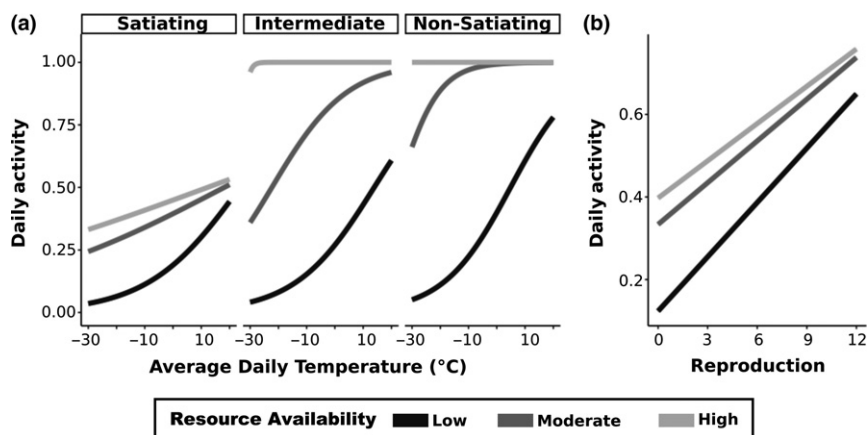


Figure 4 Predicted responses of optimal daily activity (proportion of 24 h) of red squirrels to temperature (a), and reproductive opportunities (b) across variation in resource availability and resource type (panels in A). Predictions are based on measured values of ambient temperature (T_a), resource availability (R_A), proportion of available resources that were satiating (R_T) and mating opportunities (nq) from the study area.

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 capitalises 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 mobilisation (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

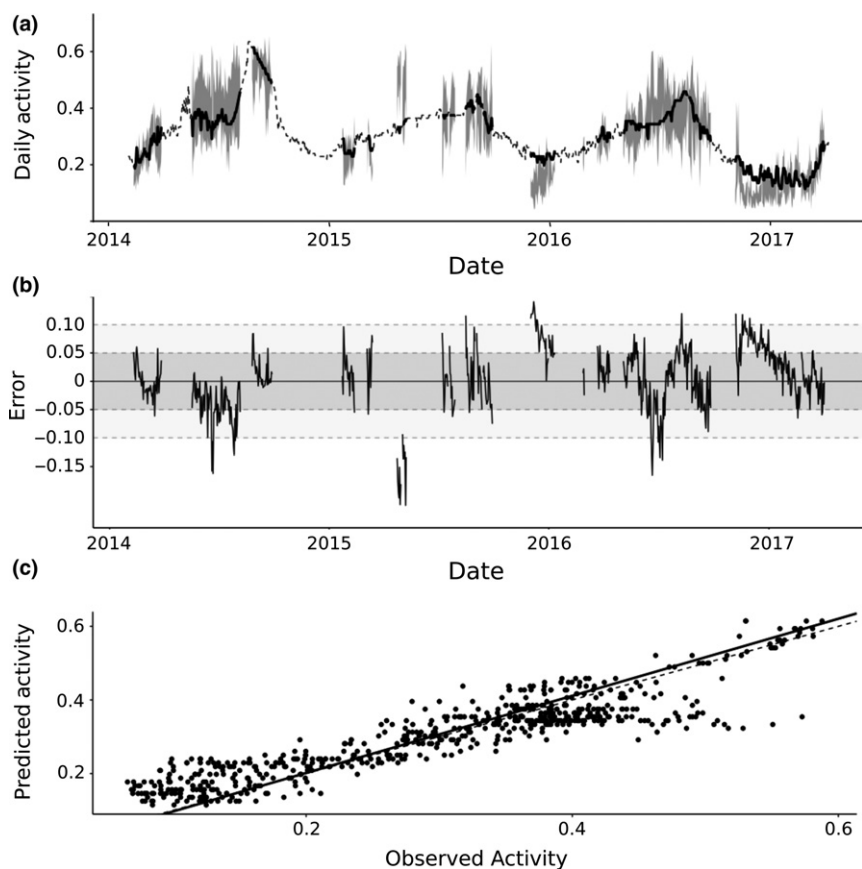


Figure 5 Observed and predicted daily activity of a population of free-ranging red squirrels in southwestern Yukon (a). Activity was observed over 3.5 years using accelerometers ($n = 489$) and predicted according to optimisation of energetic and reproductive gain in the decision between activity and 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 h of daily mean value and light grey band represents range within 2.4 h.

secondary hoarding season occurred following a spruce mast-ing 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 maximisation 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 behaviour 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 & 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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AUTHORSHIP

EKS and MMH designed the rationale for the manuscript and developed the mathematical model, EKS, AKS and ERS lead the collection of activity data, all authors assisted in the collection and maintenance of all other data, and EKS lead the analysis and writing of the manuscript with input from all authors.

DATA AVAILABILITY STATEMENT

All data is archived on figshare (<https://doi.org/10.6084/m9.figshare.11885175.v1>).

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