

1 Running head: Predicting activity over time

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

5

6 **Studd EK^{1,2*}, Menzies AK¹, Siracusa ER³, Dantzer B^{4,5}, Lane JE⁶, McAdam AG⁷, Boutin**
7 **S², and Humphries MM¹**

8

9 ¹Department of Natural Resource Sciences, McGill University, Sainte-Anne-de-Bellevue,
10 Quebec, Canada

11 ²Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

12 ³Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

13 ⁴Department of Psychology, University of Michigan, Ann Arbor, MI, USA

14 ⁵Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI,
15 USA

16 ⁶Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

17 ⁷Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA.

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19 * corresponding author: emily.studd@mail.mcgill.ca (438-863-3858)

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21 **Statement of authorship:** EKS and MMH designed the rationale for the manuscript and
22 developed the mathematical model, EKS, AKS, and ERS lead the collection of activity data, all
23 authors assisted in the collection and maintenance of all other data, and EKS lead the analysis
24 and writing of the manuscript with input from all authors.

25

26 **Data Accessibility Statement:** All data will be archived on dryad after publication.

27

28 **Keywords:** accelerometer, behaviour, decision-making, energetic gain, hoarding, metabolic
29 ecology, optimal behaviour, *Tamiasciurus hudsonicus*

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/ELE.13494](https://doi.org/10.1111/ELE.13494)

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Article Type: Letter

Word count: abstract (147), main text (4998)

Number of references: 66

Number of figures: 5

Number of tables: 0

Number of text boxes: 0

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 ($R^2=0.83$) 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.

61 **Introduction**

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

69
70 However, successful documentation of behavioural responses to environmental variation and
71 their ecological consequences has been limited by at least three major impediments.
72 Methodologically, the difficulty of quantifying animal behaviour outside of the direct presence
73 of a human observer has often constrained behavioural research to temporal extents and
74 observation windows that are much shorter than, and not fully representative of, seasonal and
75 multi-annual environmental variation (Altmann & Altmann, 2006). Empirically, behavioural
76 variation is multi-dimensional, including but not limited to movement, feeding, and social
77 behaviour (Martin & Bateson, 1993), making it challenging to characterize behavioural
78 responses in a generalized, yet ecologically-relevant manner. Finally, conceptually, the
79 importance of behaviour in defining the energetic and ecological status of animals has often been
80 misrepresented or neglected in physiological models and ecological theory. For example, the
81 metabolic theory of ecology has focused primarily on body size and temperature - but not
82 behaviour - as determinants of metabolic variation (Brown et al., 2004; Humphries & McCann,
83 2014). Meanwhile, consumer resource theory allows for behaviour to affect the consumption of
84 resources, but treats energy expenditure as behaviourally-independent (Yodzis & Innes, 1992;
85 Post et al., 2000). The methodological constraint requiring direct observation of behaviour has
86 now largely been eliminated by recent advances in biologging technologies which offer effective
87 methods for continually recording fine-scale behavioural variation (Kays et al., 2015) over long
88 durations (Williams et al., 2016; Tatler et al., 2018; Studd et al., 2019). Accordingly, we focus
89 the next two paragraphs on describing an empirical approach for categorizing behavioural
90 variation and a conceptual approach to relating these behavioural categories to their energetic
91 and ecological consequences.

92

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

102

103 Animals can be thought of as energy processors that acquire energy from the environment and
104 allocate this energy among maintenance, growth, and reproduction (Yodzis & Innes, 1992).

105 Considering animals in this way situates energetic status as the mechanistic link connecting
106 environmental variation, including that in resource availability and thermal conditions
107 (Scholander et al., 1950; Mueller & Diamond, 2001), to the survival and reproduction of
108 individuals, and the demographics of populations. In considering bioenergetic responses to
109 environmental variation, energy expenditure is often measured and modeled as behaviourally-
110 independent (Yodzis & Innes, 1992; Brown et al., 2004; Humphries & McCann, 2014).

111 However, for all animals, acquiring resources requires activity, and activity requires energy
112 expenditure (Kam & Degen, 1997; Humphries & Umbanhowar, 2007). Energetic surplus is
113 achieved only when the energy gains offered by activity exceed its energetic cost. Behavioural
114 activity is thus a fundamental, but under-appreciated, determinant of how environmental
115 variation affects the energetic status of organisms. Although other areas of research in ecology
116 and evolution consider behaviour-energetic linkages more explicitly, like the possible co-
117 evolution of metabolic and behavioural traits (i.e. metabolism and personality traits; Careau et
118 al., 2008; Biro & Stamps, 2010; Mathot & Dingemans, 2015) or the link between locomotory
119 performance and ancillary change in metabolic traits (Rezende et al., 2009; Careau et al., 2011),
120 these areas of research tend not to focus on how shared variation in activity and energetic status
121 drive ecological responses to environmental variation.

122

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

145

146 **Materials and Methods**

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

148 We used accelerometers to measure activity on 225 individual red squirrels over three and a half
149 years (2014-2017, deployments=489; squirrel-days=5066). This biologging research focuses on a
150 bottom-up regulated population in the Kluane region of southwestern Yukon (61°N, 138°W) that
151 has been the focus of long-term monitoring since 1987 (McAdam et al., 2007; Krebs et al.,
152 2014). As a free-ranging study population, red squirrels offer several advantages in documenting
153 drivers of activity variation, including year-round residency, large sample size, daily and

154 seasonally variable activity patterns (Pauls, 1977; Studd et al., 2016; Studd, Landry-Cuerrier, et
155 al., 2019), quantifiable resources (LaMontagne et al., 2005; Fisher et al., 2019), and most
156 importantly, the ability to accurately classify activity and inactivity on undisturbed individuals
157 using accelerometers (Studd, Landry-Cuerrier, et al., 2019).

158
159 Individual squirrels were captured on defended territories, weighed, assessed for reproductive
160 condition, and fitted with an accelerometer (models Axy2/Axy3, 4 g [1.7% of body mass],
161 Technosmart Europe) in collar form, either ventrally mounted on its own (n=128) or dorsally-
162 mounted in combination with a ventrally-mounted VHF radio transmitter (n=361, model PD-2C,
163 4 g [1.7% of body mass], Holohil Systems Limited, Carp, ON, Canada; see Studd et al., 2019 for
164 collar design). All accelerometers recorded acceleration between +/- 8 g_{forces} at a sampling rate of
165 1 Hz and temperature at a rate of 0.1 Hz, frequencies that have been shown to capture broad-
166 scale behaviour of small animals with high accuracy, allowing for long-duration recordings
167 (Tatler et al., 2018; Studd et al., 2019). Squirrels were released at site of capture and remained
168 free-ranging until recaptured for collar removal (3 - 103 days later). Accelerometer data was
169 processed and classified into two behavioural states, active (physically moving outside a nest)
170 and inactive (physically not moving or inside a nest) using two thresholds described in detail in
171 Studd et al (2019). Briefly, animals were in nest when the collar temperature was above the
172 threshold value from a k-means clustering of all collar temperatures recorded that day (2
173 clusters), and were moving when the 10 second sum of the changes in acceleration from one
174 second to the next was greater than 1.06 g_{forces} . We first assessed timing of activity by calculating
175 proportion time spent active during 4 different light phases: day, dusk (sunset to start of civil
176 twilight), night, and dawn (end of morning civil twilight to sunrise). Then, we calculated daily
177 activity as the proportion of 24 hours in which squirrels were active. All procedures were
178 approved by animal care committee at McGill University (Animal Use Protocol #4728) and were
179 conducted under Yukon Territorial Government *Wildlife Research Permits* and *Scientist and*
180 *Explorers Permits*.

181
182 Ambient temperature, T_a , was calculated at 15-minute intervals from recordings at nine locations
183 across or near the study site. Our index of resource availability, R_a , reflects within and among
184 year variation in the abundance and accessibility of key food sources to red squirrels and is based

185 on quantified production, hoarding, and consumption of spruce cones, the primary food source
186 for this population, in combination with direct feeding observations of alternative resources ($n =$
187 22,513). We distinguished each food source according to resource saturation characteristics (the
188 extent to which additional resource gain diminishes as resource exploitation time increases) by
189 categorizing between resources that were subject to intake saturation because they can only be
190 consumed when encountered, and those that were alleviated from short-term saturation
191 constraints because they can be hoarded for later consumption. This index of resource type, R_t ,
192 ranged from 0 when all available resources were only consumable (including previously hoarded
193 items) and 1 when all available resources are hoardable. Finally, our mating opportunities
194 variable was the product of the number of mating events each week by the probability of
195 offspring recruitment as observed annually within the population. Details of how each
196 explanatory variable was measured in the field, and subsequently calculated can be found in
197 supplementary materials 1, 2, and 3.

198

199 *Statistical Analysis*

200 We tested when within the diel period squirrels were active, and whether that changed through
201 the year using an ANOVA with an interaction between time of day (dawn, day, dusk, night) and
202 season (spring, summer, autumn, winter). Season was defined according to normalized
203 difference vegetation index values extracted for the study area from MODIS (winter: $NDVI <$
204 0.35 , spring: $0.35 < NDVI < 0.61$ and day of year < 200 , summer: $NDVI > 0.61$, autumn: $NDVI$
205 < 0.61 and day of year > 200 ; Didan, 2015). Following this analysis, we tested whether activity
206 between sunrise and sunset (represented as proportion of 24 hours) was driven by R_a , R_t , T_a ,
207 mating opportunities, or a combination of these variables by building competing GLMM models
208 for binomial data with a logit link. When testing models with combinations of variables, we
209 included a three-way interaction (R_a , R_t , T_a) and a two-way interaction (R_a and mating). Since
210 mating occurs when only non-hoardable resources are available, we split mating into two
211 variables: a 2-level categorical variable (mating or non-breeding), and a continuous variable of
212 mating opportunities which was only tested for values greater than zero when $R_t = 0$. All models
213 included random effects of squirrel ID, and observation level (to control for over-dispersion;
214 dispersion parameter ~ 1). Models were compared using AIC. Additionally, we tested the same

215 variables in a generalized linear model (binomial) of daily mean activity values to determine the
216 explanatory power of the model at explaining population level variation in activity over time.

217

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

219 We constructed an energetic and mating optimization model to assess how, in theory, daily
220 activity should respond to variation in temperature, resources, and mating opportunities if
221 animals optimize inactive and active states. A basic version of this model is described in
222 Humphries and Umanhower (2007), elaborated here to incorporate additional documented
223 drivers of red squirrel activity patterns, including diurnality (Pauls, 1977), food hoarding
224 (Fletcher et al., 2010; Archibald et al., 2013), and access to thermal refuges (Humphries et al.,
225 2005; Guillemette et al., 2009). Despite the red squirrel focus, the overall modeling should be
226 generalizable to other animals that vary behaviour in response to bottom-up drivers, because it is
227 based on commonalities of endotherm behaviour and energetics (highlighted below).

228

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

$$233 \text{ Behaviour[Active, Inactive]} (G_e, G_r) = \begin{cases} \text{Active} & \text{if } G_{ea} > G_{ei} \text{ or } G_r > 0 \\ \text{Inactive} & \text{if } G_{ei} \geq G_{ea} \text{ and } G_r = 0 \end{cases} \quad (1)$$

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

$$236 G_e = I - E \quad (2)$$

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

$$240 G_{ei} = -E_i \quad (3)$$

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

$$243 G_{ea} = I - AE_i \quad (4)$$

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

$$247 \quad E = f(T_a) \quad (5)$$

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

$$251 \quad E_a = f(T_a) \quad (5a)$$

$$252 \quad E_i = f(T_a, Q) \quad (5b)$$

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

$$262 \quad I_{(t)} = R/\alpha^{(t-1)} \quad (6)$$

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

$$269 \quad G_r = nqm \quad (7)$$

270 where n is the number of potential mating events, q is the quality of offspring produced by
271 mating, and m is a mating conversion factor equal to the rate at which activity is expected to
272 increase per unit of nq . Finally, the tendency that **organisms express periodicity in activity**
273 **patterns over a 24-hr cycle** is integrated into our model through a conditional argument

274 restricting activity to the diel period (e.g. diurnal, nocturnal) within which the species is most
275 active.

276
277 To explore optimal activity responses to a range of hypothetical temperature, resource, and
278 mating opportunity conditions, we ran a series of simulations under two main frameworks. The
279 first explored activity responses to the environmental conditions that influence G_e , by varying
280 temperature, resource availability, and resource type. The second simulations explored activity
281 responses generated by G_r , by varying mating opportunities (qm) and resource availability. See
282 supplementary materials 4 for elaborated versions of equations 1-7, and a table defining all
283 variables, units, and parameter-values used in simulations (Table S1).

284 285 **Comparing Measured and Modelled Activity Patterns**

286 We tested the ability of our model to predict animal activity using measurements of squirrel
287 resource availability, diet composition, mating events, juvenile recruitment, and air temperature
288 for R_a , R_t , n , q , and T_a respectively. After generating a predicted value for daily activity for each
289 day of the 3.5-year study duration, we assessed the correspondence of observed (measured) and
290 predicted (modelled) activity by calculating the percentage of days where predicted activity was
291 within 1.2 hours and 2.4 hours of the daily mean observed value (647 days with >3 squirrels).
292 The parameters that were not directly measured or previously known were the mating conversion
293 factor (m), the scaling of R_a , and the diminishing returns of the two resource types (hoardable
294 and non-hoardable). We set m according to the empirically observed slope between activity and
295 mating opportunities at average resource levels ($R_a=30$; $m = 0.016$). R_a was scaled
296 proportionately so the lowest resource value generated enough active gain for at least 15 minutes
297 of activity in a day at -20°C . Using measured activity, we assessed how varying the value of
298 $\alpha_{\text{Hoardable}}$ and $\alpha_{\text{Non-hoardable}}$ influenced the accuracy of our model (see Supplemental Materials 4 for
299 details).

300 301 **Results**

302 **Measured Activity**

303 Squirrels were primarily inactive at night and active during the day with some activity during
304 dawn and dusk (Fig. 1), but the amount of activity was seasonally dependent ($F=505$, $df=9$,

305 $P < 0.001$; Fig. 1a-d). Squirrels were most active in autumn, averaging 75.2% of daylight hours
306 (10.1 hours), and least active in winter, averaging 43.1% of daylight hours (3.73 hours). Activity
307 during the night averaged 2% (9 min; range 0 – 70 min) with little variation between seasons.
308 Dawn and dusk activity was generally limited (~ 5 min per period) except during autumn when
309 activity would begin during the dawn period (~ 16 min per period).

310

311 Red squirrel activity varied seasonally and multi-annually, with individual values ranging from 1
312 hour to 15.5 hours per day (Fig. 2). The models with the most support (weight = 1) explained
313 approximately 13% of the variation in activity at the individual level (conditional $R^2 = 0.13$;
314 Table S2) and 88% of daily activity variation observed at the population level (adjusted $R^2 =$
315 0.88). Activity was dependent on interacting effects of resource availability, resource type, and
316 air temperature ($z = 356.8$, $p < 0.001$). The lowest activity levels occurred when cold
317 temperatures coincided with low availability of non-hoardable resources, and the highest activity
318 levels occurred when warm temperature coincided with high availability of hoardable resources
319 (Fig. 3a). Activity generally decreased as temperature decreased below 10°C , decreased or
320 remained constant at temperatures above 10°C , increased with increasing resource availability,
321 and increased as the proportion of hoardable resources increased (Fig. 3a). However, the strength
322 of the activity response to these three environmental variables was inter-dependent. For example,
323 when resources were non-hoardable (strongly saturating), increased resource availability reduced
324 the effect of temperature on activity, and when resources were hoardable (weakly saturating),
325 increased resource availability increased activity regardless of temperature (Fig. 3a). Activity
326 response to mating opportunities was dependent on resource availability. Males during the
327 mating season had higher activity than non-breeding males and females (Fig. 3b; $z = 5.57$,
328 $p < 0.001$). Among breeding males, activity increased with increasing reproductive opportunities
329 ($z = 2.01$, $p = 0.04$), with indications, although not significant, that the strength of this response
330 might increase as resource availability decreases (Fig. 3b; $z = -0.25$, $p > 0.05$).

331

332 **Modelled Activity**

333 Our model predicted that activity increased exponentially as daily mean temperature (T_a)
334 increased and approached the thermal neutral zone of an endotherm. Increasing resource
335 availability resulted in increased activity but the extent of that increase was dependent on

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

350

351 **Comparing Measured and Modelled Activity Patterns**

352 Our model with diminishing return values set to the best fit ($\alpha_{\text{Hoardable}} = 1.10 - 1.12$, $\alpha_{\text{Non-hoardable}} =$
353 $1.09 - 1.35$) predicted squirrel activity within 1.2 hour of the observed daily mean 59.8% of the
354 time and within 2.4 hours of the mean 92.6% of the time (Fig. 5a, b). Predicted activity values
355 were highly correlated with observed values ($R^2 = 0.83$) suggesting that overall the model
356 accurately captured the seasonal and multi-annual variation in squirrel activity (Fig. 5c).
357 However, the model tended to over-estimate the lowest activity levels, and failed to capture one
358 period of high activity (spring 2015). Adjusting diminishing return values of hoardable and non-
359 hoardable resources changed the accuracy of predicting activity within 2.4 hours of observed
360 values (accuracy range = 0-0.926 %; Supplementary Materials 5, Fig. S3) but had minimal
361 influence on the correlation between predicted and observed values (R^2 range = 0.609 to 0.83).

362

363 **Discussion**

364 We demonstrated that the vast majority of multi-seasonal and multi-annual variation in activity
365 can be explained by an energetic-based behavioural choice model that incorporates only resource
366 availability and quality, air temperature and presence of mating opportunities. Our analyses

367 suggest that activity reflects an optimization of energetic and reproductive gain, with individuals
368 active when the gains of activity outweigh the gains (or minimization of losses) offered by
369 inactivity. Based on this optimality approach, the activity responses of free-ranging red squirrels
370 to abiotic and biotic drivers became highly predictable, when aggregated at the level of a day.
371
372 Incorporating resource type, air temperature, and reproductive parameters into an activity
373 optimization model predicts that activity responds dynamically to environmental conditions.
374 Increasing resources, increasing ambient temperature, or decreasing resource saturation rates all
375 led to increases in activity. However, both red squirrel activity and our predictive model
376 highlighted the inter-dependency of activity responses to temperature and resources. This
377 interacting effect is driven by resources and temperature influencing opposing components of net
378 energy gain (i.e., resources on intake, and temperature on expenditure), and illustrates that
379 organisms can buffer some environmental variability if either intake can be increased or
380 expenditure decreased (King & Murphy, 1985; Boggs, 1992; Williams et al., 2015). An ability to
381 buffer the environment helps to explain why activity responses to resources and/or temperature
382 vary between studies (Fernandez-Duque, 2003; Murray & Smith, 2012; Hall & Chalfoun, 2019)
383
384 Among the environmental drivers we considered, resource type appeared to be the strongest
385 driver of activity variation. The energetic value and potential hoardability of different resource
386 types are known to be key components of short term foraging decisions (Pyke et al., 1977;
387 Gerber et al., 2004; Lichti et al., 2017). Our results extend these patterns across much longer
388 time scales, to show how resource abundance and saturation drive daily activity levels across
389 seasons and years. In red squirrels, we distinguished resources according to whether they could
390 be hoarded (i.e., weakly saturating) or not (i.e., strongly saturating) and the model confirmed the
391 importance of this distinction. From an ecological perspective, non-saturating foraging returns
392 for hoardable resources drives high rates of sustained activity for as long as this resource type
393 remains abundant. Although we only focused our categorization of resource type on the
394 distinction between hoardable and non-hoardable resources, additional resource type differences
395 would need to be considered in systems where, for example, energetic values, nutrient
396 composition, or handling constraints vary more and have stronger effects on activity
397 optimization (Emlen, 1966; Pyke et al., 1977; Gill, 2003).

398

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

411

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

427

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

439
440 Despite its simplicity, we show that energy-based optimality models of behaviour can have a
441 surprisingly powerful ability to predict activity variation expressed by individuals
442 over seasonal and annual time frames. Some of the activity responses to environmental variation
443 described here, like reduced activity in winter, when resources are scarce, days are short, and air
444 temperatures are cold, may seem unsurprising, but are also indicative that behavioural decisions
445 are based on a maximization of energetic gain rather than a maintenance of energy balance
446 (which would cause activity to increase, instead of decrease, as resources or temperature
447 decreases). Our analyses also revealed several, less obvious patterns, including autumn activity
448 peaks driven more by resource type than resource abundance, the resource-dependency of
449 activity responses to temperature and mating opportunities, and activity peaks not predicted by
450 the model used to identify novel, season-specific forms of activity. Additionally, we show that
451 aggregation of behavioural variation to a daily scale was critical to predictive success; our model
452 predicted 83% of variation in daily activity expressed across seasons and years, but if we
453 attempted to predict whether any given individual was active at any given moment, across the
454 same multi-annual extent, explanatory power dropped to less than 15%. It thus appears, that at
455 the scale of days, seasons, and years, the energy and reproductive requirements of populations
456 coalesce with constraints imposed by the abiotic and biotic environment to drive highly
457 deterministic and predictable activity responses. Whereas, within these days and seasons, at the
458 scales of minutes to hours, individuals retain considerable flexibility in choosing what to do and

459 where to be at any one moment in time. Intriguingly, if we as researchers can predict squirrel
460 behaviour using relatively few variables and a relatively simple model, perhaps so too can
461 predators, which presumably know them better. This may cause predators to structure their
462 activity patterns according to these expectations, which in turn may select for variability in
463 behaviour around the central tendencies documented here. This could account for the
464 unpredictability of behavior at finest temporal scales. We hope that the opportunity to combine
465 activity-and energy-explicit optimality modelling with biologging of activity patterns expressed
466 across seasons and years enables broader evaluation of the importance of behavioural variation
467 in seasonal and annual energetic status, population dynamics, and trophic interactions. As also
468 described in Humphries and McCann (2014), this may include extending how we think of
469 metabolic theories in ecology, beyond equations focused on size, temperature, and metabolic rate
470 (Brown et al., 2004), to include equations focused on energy balance, energy flows, and the
471 ecological importance of both metabolic and behavioural variation.

472

473 **Acknowledgements**

474 We thank Agnes MacDonald for long-term access to her trapline, and to the Champagne and
475 Aishihik First Nations for allowing us to conduct work on their traditional territory. We thank all
476 the volunteers, field assistants and graduate students who helped directly with this fieldwork or
477 as part of the KRSP data collection. Thank you to Alice Kenny and Charles Krebs for running
478 CEMP and supplying on-site temperature data. Technosmart was incredibly helpful through this
479 project with troubleshooting accelerometers. Funding was provided for this project by the
480 Natural Sciences and Engineering Research Council, W. Garfield Weston Foundation, Institut
481 Nordique du Quebec, and National Science Foundation. This research is publication number XX
482 for the Kluane Red Squirrel Project.

483

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665

666 Figure 1. Seasonal variation in observed red squirrel (n=225) activity and inactivity throughout
667 the day recorded using accelerometers. The timing and amount of activity varies according to
668 each season (spring (A), summer (B), autumn (C), and winter (D)). Timing of daily activity is
669 presented as proportion of photoperiod phase that squirrels were active (left), along with an
670 actogram illustrating how activity (black) is organized within each time period (right). Each day
671 is subdivided into four photoperiods in each figure: dawn (light grey shading in actogram), day
672 (white), dusk (light grey) and night (dark grey) with the relative length of each phase represented
673 by the width of box. Actograms display 7 days of activity and inactivity for a randomly selected
674 individual.
675

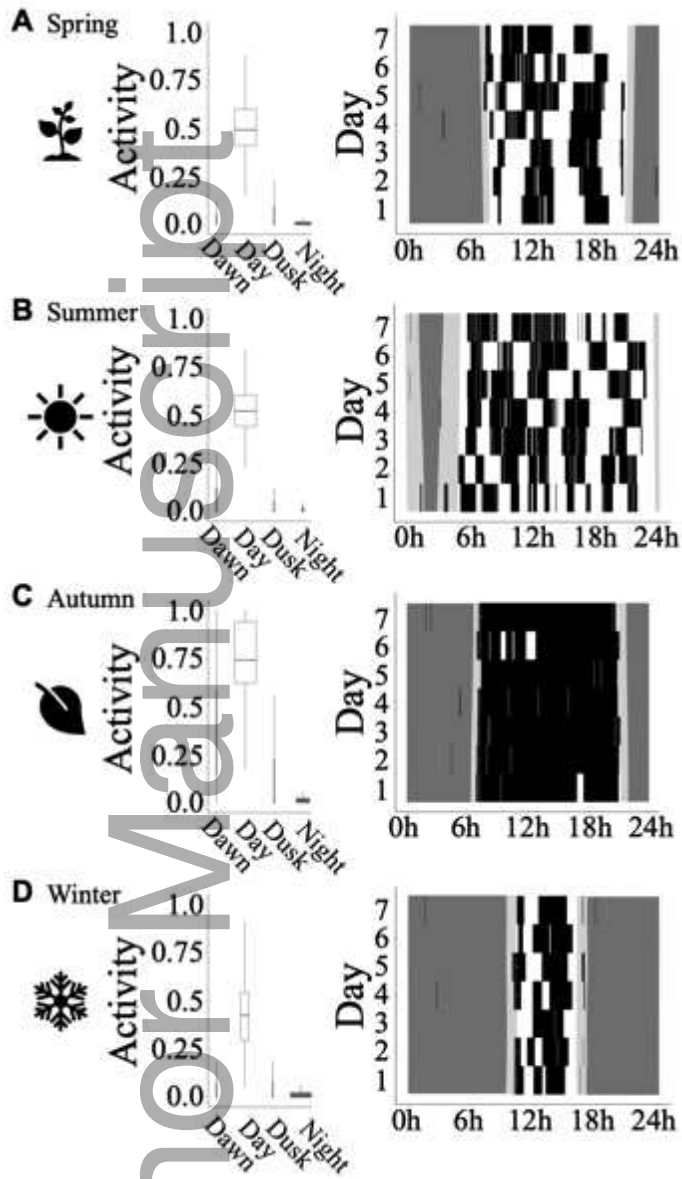
676 Figure 2. Observed daily activity (proportion of 24 hours) of free ranging red squirrels ($n = 225$)
677 recorded using accelerometers over three and half years. Each date is represented as a boxplot
678 denoting the 25 and 75 quantiles with dots representing activity outside that range.

679
680 Figure 3. Daily activity (proportion of 24 hours) responses to temperature, resources, and
681 reproductive opportunities. The effects of temperature on activity were dependent on resource
682 availability and resource type (A), while the effects of mating opportunities were dependent on
683 resource availability (B). Responses and 95 confidence intervals were generated from a GLMM
684 of 3.5 years of activity data collected from accelerometers. Resource availability at a saturation
685 (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
686 (moderate), and 120 (high) to represent the natural range observed at each condition. As mating
687 only occurs when $R_T = 0$, resource availability values were 5 (low), 20 (moderate), and 40
688 (high).

689
690 Figure 4. Predicted responses of optimal daily activity (proportion of 24 hours) of red squirrels to
691 temperature (A), and reproductive opportunities (B) across variation in resource availability and
692 resource type (panels in A). Predictions are based on measured values of ambient temperature
693 (T_a), resource availability (R_A), proportion of available resources that were satiating (R_T), and
694 mating opportunities (nq) from the study area.

695
696 Figure 5. Observed and predicted daily activity of a population of free-ranging red squirrels in
697 southwestern Yukon (A). Activity was observed over 3.5 years using accelerometers ($n=489$)
698 and predicted according to optimization of energetic and reproductive gain in the decision
699 between activity and inactivity. Predictions (black) are overlaid on range of observed daily
700 activity (light grey shading). The correspondence between observed and predicted is assessed by
701 the error of the prediction relative to the observed daily mean value (B), and the correlation of
702 predicted daily values to observed (C). Error of the prediction is the difference between the
703 observed mean daily proportion of activity and model predicted daily proportion (convertible to
704 hours by multiplying by 24; B). Dark grey band represents within 1.2 hours of daily mean value
705 and light grey band represents range within 2.4 hours.

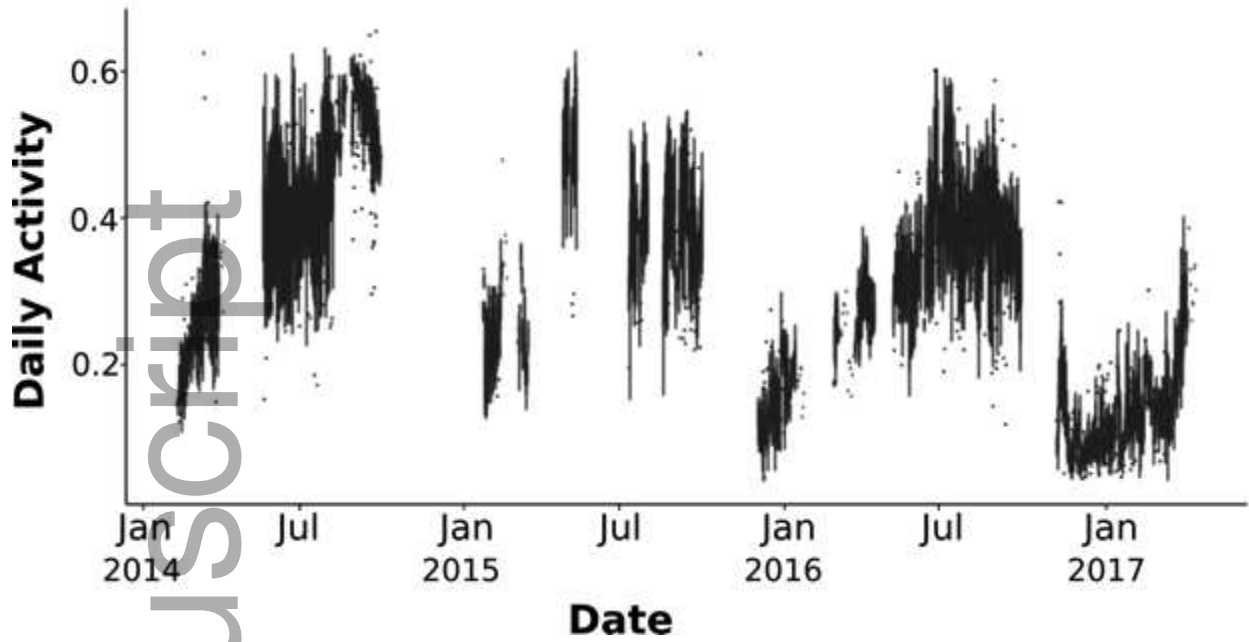
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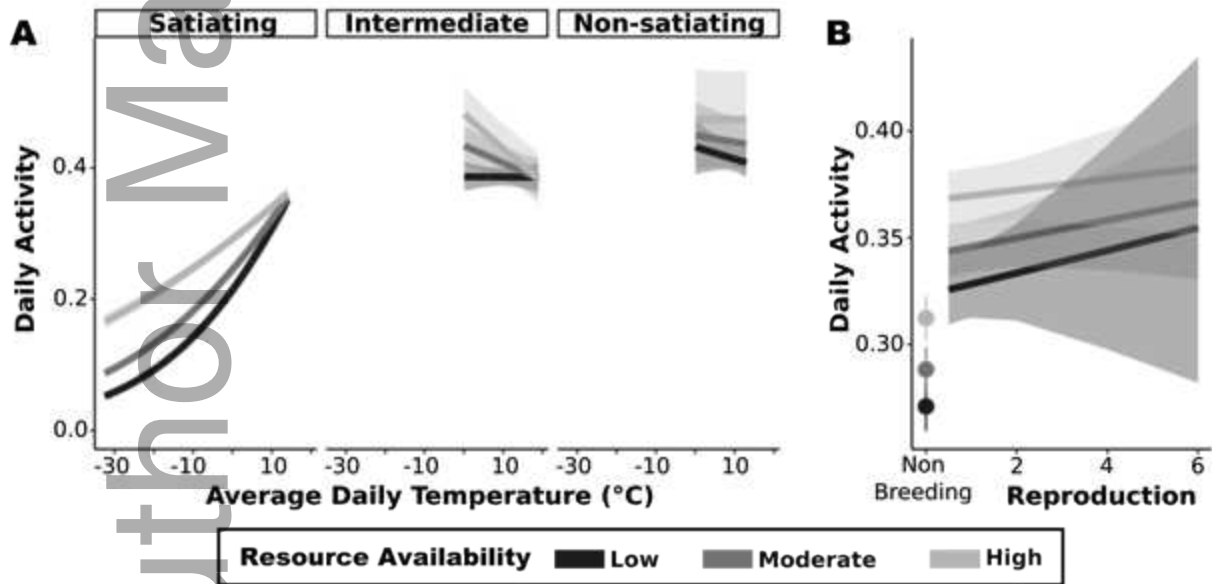
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709 Fig. 1

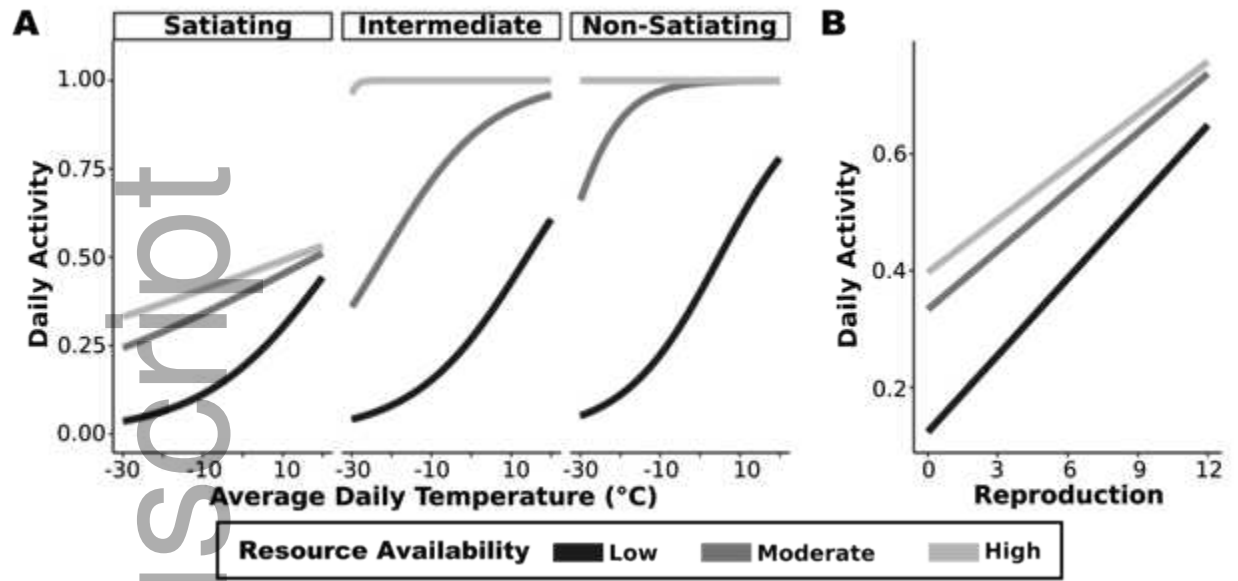
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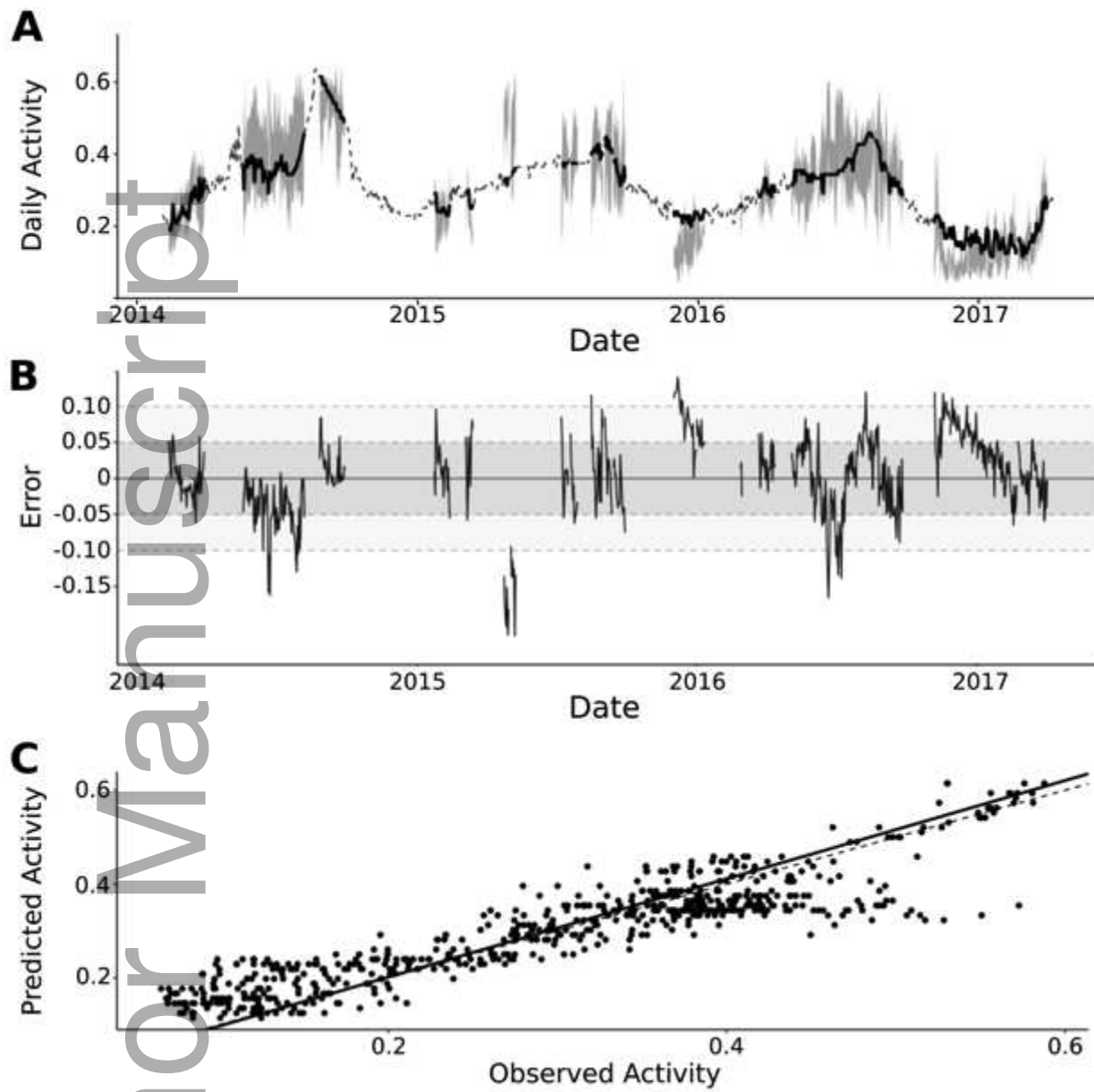


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719 Fig. 4

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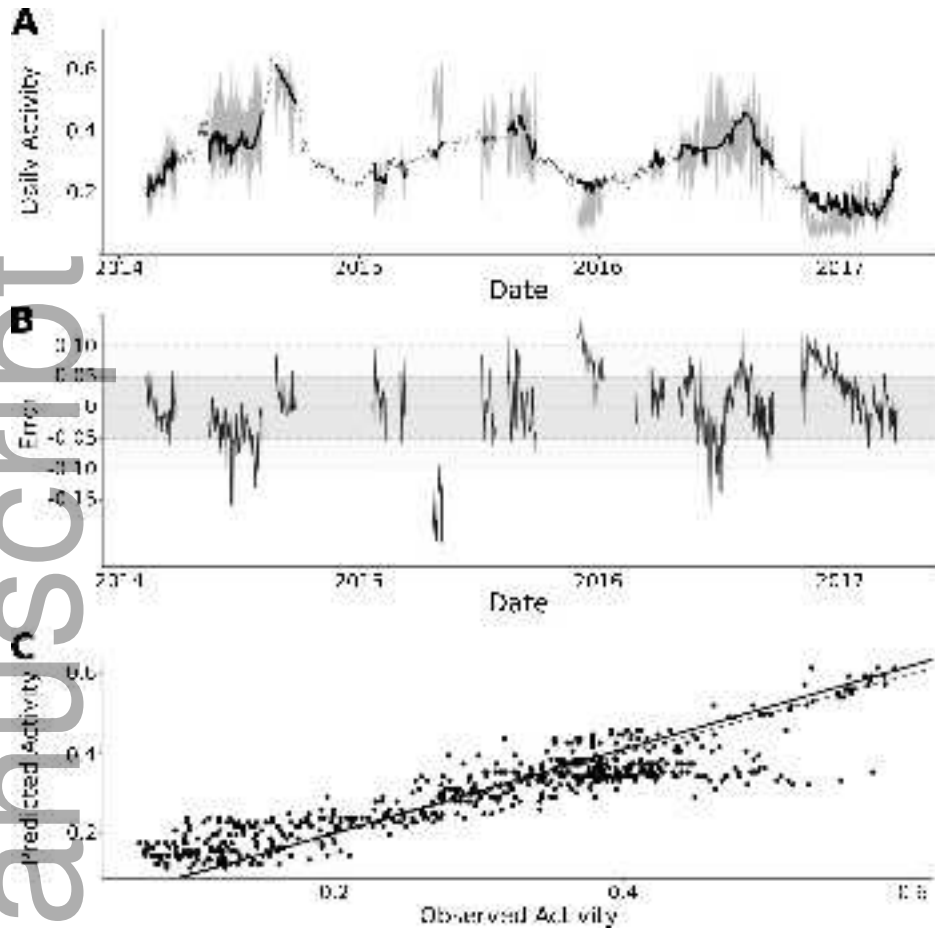
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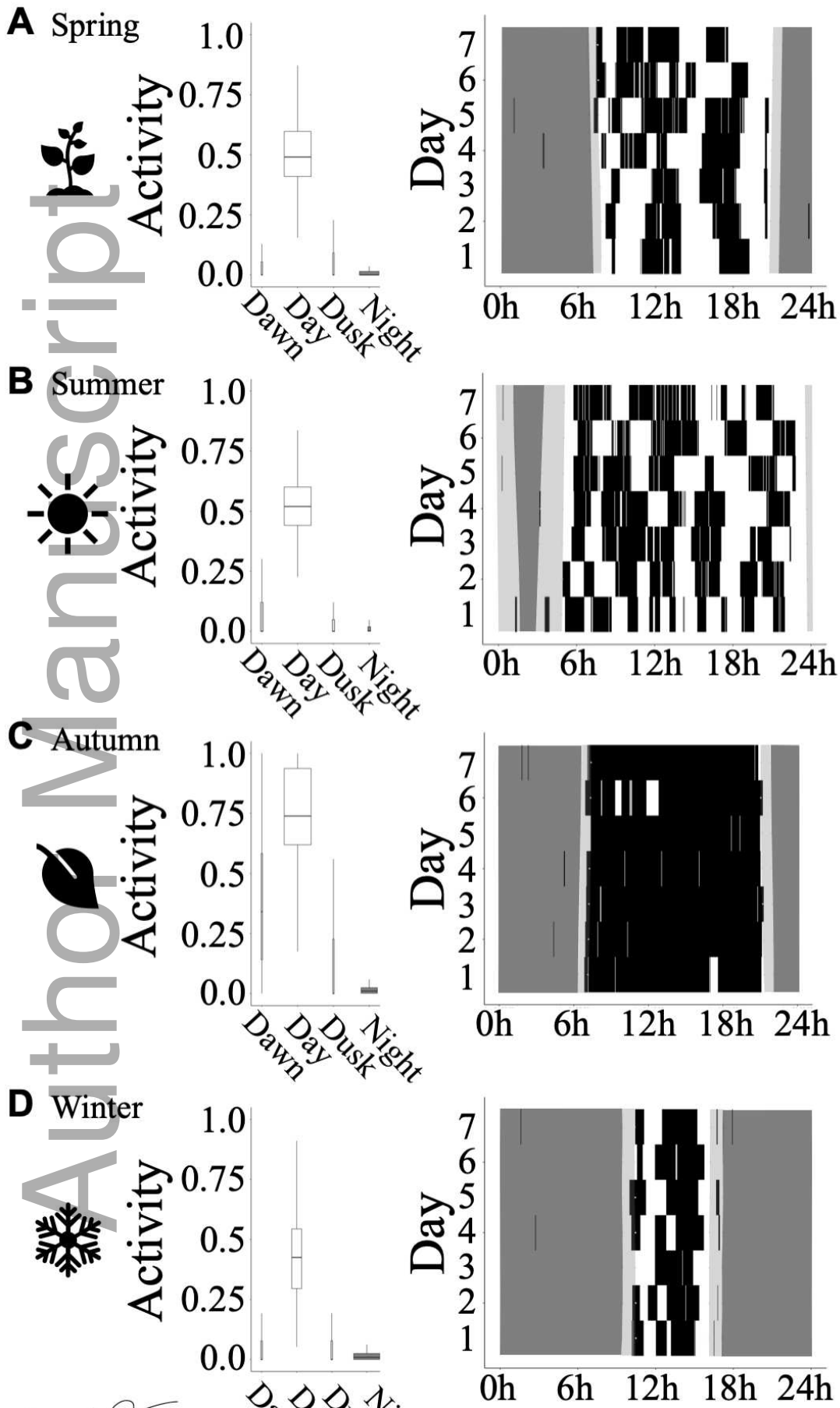
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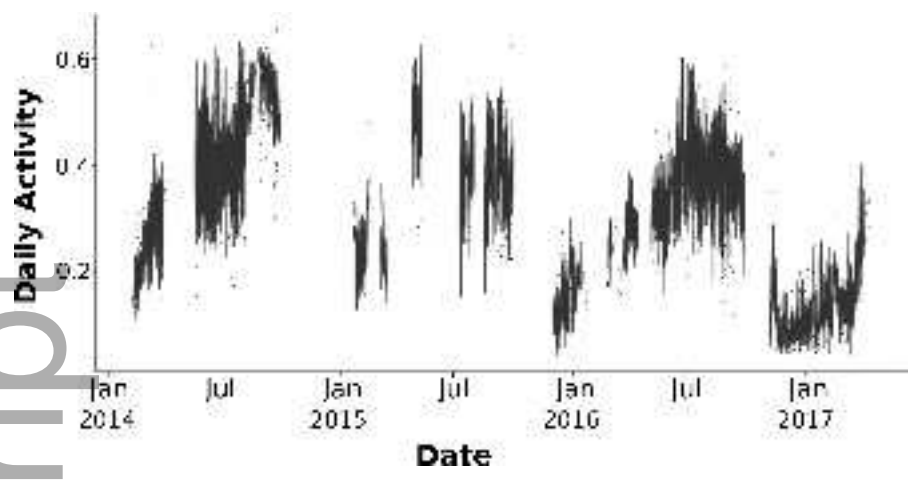
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Fig. 5.

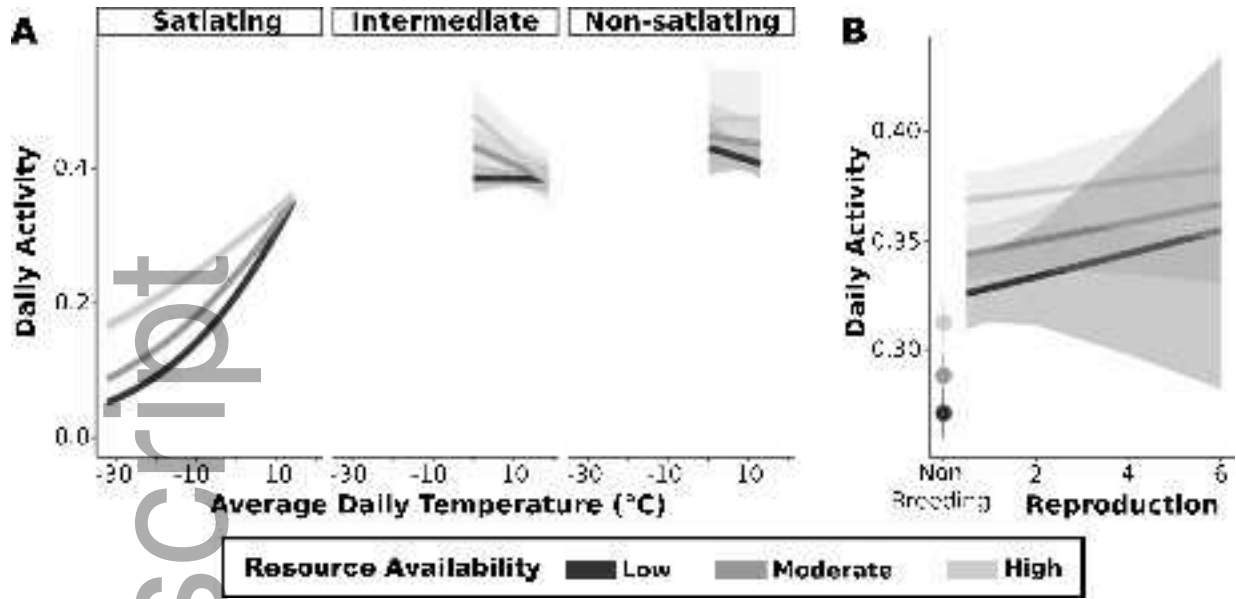


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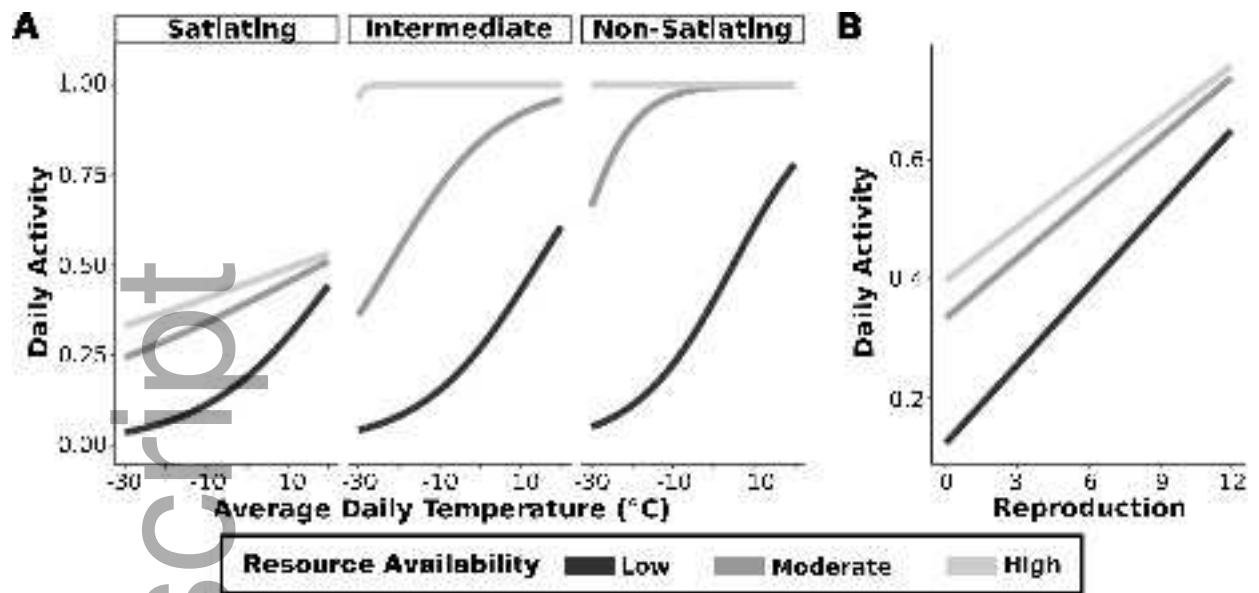




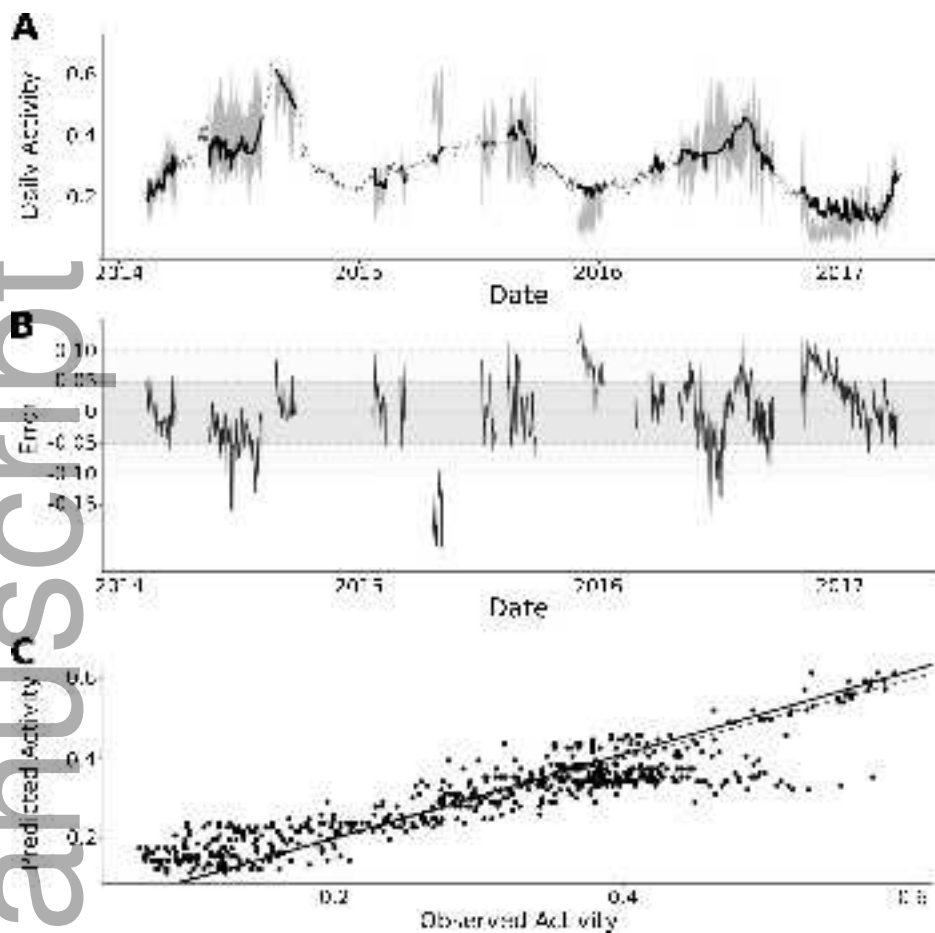
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