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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Behavioural adjustments of predators and prey to wind speed in the boreal forest

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Abstract

Wind speed can have multifaceted effects on organisms including altering thermoregulation, locomotion, and sensory reception. While forest cover can substantially reduce wind speed at ground level, it is not known if animals living in forests show any behavioural responses to changes in wind speed. Here, we explored how three boreal forest mammals, a predator and two prey, altered their behaviour in response to average daily wind speeds during winter. We collected accelerometer data to determine wind speed effects on activity patterns and kill rates of free-ranging red squirrels ($n = 144$), snowshoe hares ($n = 101$), and Canada lynx ($n = 27$) in Kluane, Yukon from 2015 to 2018. All 3 species responded to increasing wind speeds by changing the time they were active, but effects were strongest in hares, which reduced daily activity by 25%, and lynx, which increased daily activity by 25%. Lynx also increased the number of feeding events by 40% on windy days. These results highlight that wind speed is an important abiotic variable that can affect behaviour, even in forested environments.

Keywords Behavioural responses · Environmental variation · Predator detection · Predator–prey · Terrestrial · Thermoregulation

Introduction

Wind speed, an understudied component of weather that is predicted to change with climate change, can influence animal activity and trophic interactions (Cherry & Barton 2017). Over the last 30 years, wind speeds have decreased by 5–15% in most continental locations, a trend that is expected to continue into the future (Vautard et al. 2010; McVicar et al. 2012). However, relative to other aspects of weather, such as temperature, the impact of wind speed on species and species interactions has received limited attention (Cherry & Barton 2017). Previous work highlights that variation in wind speed can alter dispersal (Cáceres & Soluk 2002), activity patterns (Møller 2013; Kogure et al. 2016), species interactions (Hagemoen & Reimers 2002), and predator–prey dynamics (Quinn & Cresswell 2004; Barton 2014). The majority of this work, however, focusses on systems where wind is a major component of the local environment, or where wind directly affects locomotion (e.g., aerial species; Fairbanks & Dobson 2007; Cherry & Barton 2017; Togunov et al. 2017). Comparatively, we know little about how animals residing in forested environments respond behaviourally to fluctuations in average wind speed.

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The most commonly considered effects of wind speed involve alteration of locomotion (Weimerskirch et al. 2000; Leihy & Chown 2020) or thermoregulatory costs (Cuyler & Øritsland 2002; Boyles & Bakken 2007; Mitchell et al. 2018). The less-considered effect of wind speed on wildlife is its alteration of signal (odour, sound) transmission and reception that is critical for conspecific communication (Luther & Gentry 2013; Velilla et al. 2020), and predator–prey detection and avoidance (Hayes & Huntly 2005; Hollén et al. 2011) as highlighted in the olfactory concealment theory (Conover 2007). Depending upon the direction and strength of wind, transmission of signals will be directly aided, diminished, or made erratic, creating a skewed and sometimes unpredictable detection field around an individual (Conover 2007; Togunov et al. 2017; Holt & Butler 2019). Detection is also hindered as low-frequency 'noise' generated by wind passing over vegetation and substrate edges can mask acoustic signals, and moving vegetation can mask detectability of movement of other animals (Brumm & Slabbekoorn 2005; Pijanowski et al. 2011; Jakosalem et al. 2013). On the other hand, detection could be aided by increasing wind as is the case with flow of odour plumes through forested locations which are streamlined and made less variable with strong winds (Fogarty et al. 2018).

Due to the multifaceted effects that wind can have, the implications for animals will vary with where they reside. In open habitats, animals directly experience the full force of the wind making thermoregulatory, locomotory, and cue transmission effects key drivers of responses (Zerba et al. 1999; Ord et al. 2007; Weimerskirch et al. 2012; Leihy & Chown 2020). However, in closed or forested habitats, vegetation creates barriers to the wind reducing its direct impact; wind is unable to completely penetrate into the forest with speeds within a patch being 80% lighter than in the open (Chen et al. 1993; Davies-Colley et al. 2000). Since most forest-dwelling mammals live where there is maximum protection from wind (e.g., at ground level; Moon et al. 2019), effects of wind speed on locomotion and thermoregulation may be of lesser importance, but effects of acoustic noise generated by wind passing through the canopy, and altered flow of odour plumes by tree trunks could be substantial (Yip et al. 2017; Fogarty et al. 2018). Surprisingly though, little is known about the consequences of wind speed on forest-dwelling organisms.

Here, we examine how two forest-dwelling prey, snowshoe hares (*Lepus americanus*) and North American red squirrels (*Tamiasciurus hudsonicus*), and their shared predator, Canada lynx (*Lynx canadensis*), respond behaviourally to changes in average daily wind speed across multiple years. We compare responses between species to address two general questions. First, do terrestrial mammals living in forested landscapes show measurable behavioural responses to changes in wind speed and if so, does the magnitude of this response vary among species? Second, are these responses suggestive of thermoregulatory or sensory underlying mechanisms? Although all three species are active year-round, squirrels are active in trees, and use well-insulated arboreal nests as thermal and predator refugia (Humphries et al. 2005; Guillemette et al. 2009), while snowshoe hares and lynx are almost always found at ground surface and do not make use of thermal refugia (Graf & Sinclair 1987). Thus, we might predict that squirrels may be less sensitive to wind speed relative to hares and lynx and that most responses will be to the effects of wind on sensory mechanisms that are important for predator–prey detection.

Methods

Study area

This study was conducted in the Kluane Lake region of southwestern Yukon, Canada (61° N, 138° W), in a broad glacial valley bounded by alpine areas and bisected by the Alaska Highway. The boreal forest in this area is comprised primarily of white spruce (*Picea glauca*) interspersed with patches of trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The climate is cold continental, with snow cover occurring from October to May, and daily average temperatures and wind speeds during our study ranging from – 34.4 to 23.2 °C (90th quantiles: – 21.5 and 17.0 °C) and 0.0 to 27.0 km/hr (90th quantiles: 0.9 and 12.6 km/hr), respectively. During the study hares were at relatively high densities, meaning that winter lynx diet would be primarily composed of hares (~ 94.4%; O'Donoghue et al. 1998; Peers et al. 2020).

Measuring activity

We captured adult red squirrels (79 individuals; 118 collars) and snowshoe hares (87 individuals; 523 collars) of both sexes during winter from 2014 to 2019 using Tomahawk live-traps (Tomahawk Live Trap Co. Tomahawk, WI, USA) either baited with peanut butter (squirrels) or alfalfa and rabbit chow (hares). To match diel activity patterns, we trapped squirrels during the day and hares during the night. Adult lynx (27 individuals; 41 collars) of both sexes were captured day and night during the winter (Nov–Apr) from 2015 to 2018 using custom-made box traps (similar to design by Kolbe et al. (2003)) baited with castor oil, meat, and reflective objects. All adult individuals were fitted with an accelerometer (model Axy3 or Axy4, Technosmart, Rome, Italy, 4 g) in combination with a VHF (squirrel: Holohil, 4 g; hare: Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2 M, Holohil, Canada, both 27 ± 1 g) or GPS collar (lynx: Model Iridium GPS, Followit, Sweden, 400 g or Model Remote Download GPS, Telemetry Solutions, USA, 350 g). In all cases, accelerometers rested on the dorsal surface of the neck and recorded acceleration at 1 Hz with a resolution of ± 8 $g_{force,}$ and temperature at 1 Hz. Collars remained on free-ranging individuals until they were retrieved through recapture, after mortality (prey only), or at a scheduled collar drop-off date (lynx only). The research was completed under approval of research and animal care permits (see SI1).

Accelerometer data were converted into behavioural states according to species-specific classification algorithms. Red squirrel acceleration and temperature data (1926 days) were classified into five states (in a nest, out of a nest and not moving, travelling, foraging, and feeding) using a decision tree previously validated with direct observation at high accuracy (70.6%; see Studd et al. 2019b and S2 for details). Snowshoe hare acceleration data (6581 days) were classified into 4 states (long not moving, short not moving, foraging/feeding, and travelling) using a decision tree previously validated with an 88% accuracy at correctly classifying direct observations of captive hares (see Studd et al. 2019a and S2 for details). Although behavioural categories were not identical between the two species, we calculated daily activity as the sum of time spent travelling, foraging, and feeding in red squirrels, and time spent travelling and foraging/feeding in snowshoe hares. An index of vigilance was calculated as time spent out of nest and not moving in red squirrels (Dantzer et al. 2012), and time spent in short duration not moving bouts (defined as <5 min) in snowshoe hares. Lynx acceleration data (1405 days) were classified into four behavioural states (not moving, travelling, feeding, and grooming) using a random forest algorithm previously validated with known behavioural data to high accuracy ($F1=0.96$; Studd et al. 2021). For lynx, activity was calculated as the sum of travelling, feeding, and grooming each day, and the number of feeding events was defined as the number of times there was a clustering of feeding lasting at least 15 min and separated from any other feeding by at least 10 min. As consumption of squirrels takes less than 15 min, these feeding events only capture consumption of hares (Studd et al. 2021).

Measuring wind speed

Wind is created by uneven warming of earth's surface. When the landscape is unfrozen, observed wind patterns are a combination of weather systems, and locally generated wind from solar radiation warming large water bodies or melting glaciers (Fig. 1a). However, when the landscape is frozen, the contribution of locally generated wind is diminished, leaving wind patterns that are driven by large-scale weather systems that create fluctuations over the scale of days and not hours (Fig. 1b, c) and that are highly correlated across a region (Supp. Figure S1). Thus, wind speed patterns during winter are accurately captured by regional weather stations and locally predicted using global meteorological models with high precision. We used this information to capture changes in average daily wind speed and relate this to daily activity patterns. For most animals, a day as a unit of measure captures both active and inactive diel phases, and thus is the scale at which an organism will be balancing energy expenditure. While variation in activity at smaller time scales may reflect the effects of the immediate local environment, variation from 1 day to the next provides insight into the cumulative ecological implications on energy balance of environmental change (Studd et al. 2020). Thus, as a first step towards understanding the potential effects of wind on behaviour, we addressed our questions at the scale of average daily wind speeds and daily activity over the winter months (Oct–Mar) when microscale variation in wind and the correlation between wind and solar radiation is greatly diminished.

Daily average wind speed and temperature were calculated from hourly data recorded at the nearest weather station to the field site that was operational for the entire duration of the study (located ~ 40 km away; Haines Junction, Environment Canada) which matched well with predictions for the study site from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5-Land global model (Muñoz Sabater 2019); $R^2=0.8$). We report analyses using the Haines Junction data but also provide similar analyses using the outputs from the ECMWF model in the supplementary materials.

Statistical analysis

For all three species, we analyzed behavioural responses to wind in winter using generalized additive mixed-effects models (using bam in mgcv v1.8-33 in R; Wood 2017) with a seasonal tensor smooth using thin-plate regressive splines of week and year to capture seasonal variation in behaviour driven by a combination of resources and reproduction (Menzies et al. 2020; Studd et al. 2020). Models also included a smooth factor interaction of individual ID and week, and an autoregression variable (to account for temporal auto-correlation) starting with the first day of data for each individual and year (see S3 for details on parameters). Depending upon the model, wind and temperature were either included as individual thin-plate regressive splines or as a tensor smooth using thin-plate regressive splines of daily mean temperature and wind speed (i.e., interaction). For each species and behaviour, we compared hypothesis-driven models fit with maximum likelihood via AIC (Symonds & Moussalli 2011). In the prey species, we explored models of three different behavioural responses to wind: (1) overall daily activity (foraging and travelling),

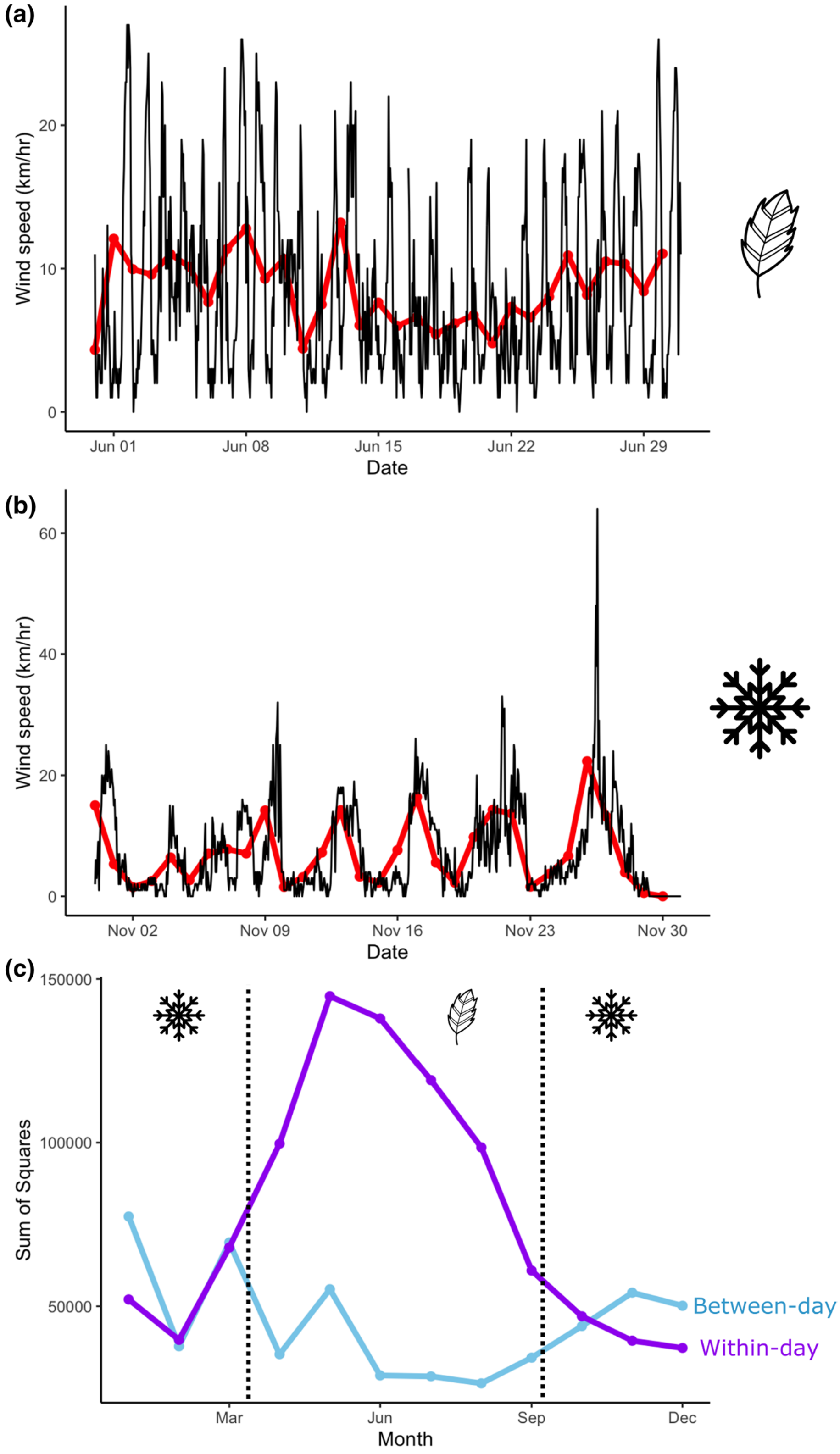

Fig. 1 Hourly variance in wind speed varies across the year at Haines Junction, YT. During summer (**a**), hourly wind speeds (black) are driven by a combination of weather systems and daily patterns in solar radiation and evaporation causing greater within day variance than between day variance in wind speeds (**c**). While when the world is frozen (**b**), hourly wind speeds are driven by continental weather systems and vary less within a day than between days (**c**). Daily mean wind speed (red line) is thus a good summary of wind conditions over a day during winter but not during summer

(2) time spent travelling (behaviour for which detection of environment is most hindered and thermal costs are highest), and (3) proportion of active time that was spent not moving—an index of vigilance. For Canada lynx, we assessed the effect of wind speed on (1) overall daily activity, (2) daily time spent travelling, and (3) the number of feeding events per day. In all cases, we compared (1) our null model that included only the seasonal tensor spline and

smooth factor individual ID term to (2) a thermoregulatory model (null model + air temperature), (3) a wind model (null model + wind), (4) a non-interaction wind model (null model + air temperature + wind), and (5) a full model (null model + temperature*wind).

Results

Both prey (red squirrels and snowshoe hares) and their shared predator (lynx) adjusted behaviour as daily wind speeds increased; however, the direction and magnitude of responses varied between species. Red squirrel behavioural responses to increased daily wind speeds were the weakest of all three species, only explaining small amounts of the variance in daily activity (0.5%) and time spent travelling (1.2%) in winter. Responses to wind in daily activity were temperature-dependent (Table S4.1; $F = 10.2$, $n = 1926$, $P > 0.001$) with larger reductions in activity to increasing daily wind speed when temperatures were colder (~ 25%; 1 h) than when warmer (~ 0%; Fig. 2a). Squirrels reduced daily time spent travelling by up to 25% (4–5 min; $F = 19.694$, $n = 1926$, $P < 0.001$) as daily wind speeds increased from 0 to 25 km/hr with responses being temperature independent (Table S4.1). While there was considerable variation around responses in activity and travelling to wind speed (Fig. 2a), squirrel responses to increasing daily wind speeds in the amount of daily vigilance (not moving behaviour when out of the nest) relative to activity were stronger and more consistent. Daily wind speeds explained 4.5% of observed variance in this behaviour. Changes in vigilance were nonlinear with the presence of two thresholds ($F = 18.7$, $n = 1926$, $P < 0.001$; Fig. 2a). The amount of vigilance was lowest when there was no wind but quickly increased to 0.1 min per minute of activity with the presence of wind. Wind speeds above this initial threshold had minimal effects on vigilance until daily average wind speeds increased above 15 km/hr, at which point squirrels drastically increased their time spent vigilant (> 0.7 min/min of activity). The extent of this response to high daily wind speeds was temperature-dependent ($F = 8.54$, $n = 1926$, $P < 0.001$; Fig. 2a) with greater vigilance at cold temperatures (10 × more vigilant than when there is no wind) than at warm temperatures (6 × more vigilant than when there is no wind). All behavioural responses by squirrels were similar when analysis used ECMWF modelled wind speed data for the study area as compared to when Haines Junction weather station data were used (Supp. Figure S4.1).

Snowshoe hare behavioural responses to wind speed were substantial with larger effect sizes than red squirrel responses (Table S4.1). Average daily wind speed accounted for 6.5%, 0.4%, and 3.6% of the variance observed in snowshoe hare daily activity, daily travel, and daily vigilance rate, respectively. Hares decreased daily activity by 25% (> 2 h) as daily wind speeds increased from 0 to 15 km/hr, and by up to 65% (~ 7 h) as daily wind speeds increased above 15 km/hr (Fig. 1b; $F = 840.5$, $n = 6411$, $P < 0.001$). The strength of this negative response increased as temperatures decreased ($F = 30.0$, $n = 6411$, $P < 0.001$). While the majority of the reduction in activity was likely due to a reduction in foraging, hares also reduced travel by 15% from 15 min/day to 12.5 min/day as wind increased from 0 to 25 km/hr (Fig. 2b; $F = 17.6$, $n = 6411$, $P < 0.001$) regardless of temperature (Table S4.1). Hares doubled the amount of short not moving events during their active period as daily wind speed increased from 0 to 25 km/hr suggesting an increase in vigilance (Fig. 2b; $F = 179.7$, $n = 6411$, $P < 0.001$). This increase in vigilance with increasing daily wind speed was temperature-dependent with Haines Junction wind data (Table S4.1; $F = 34.9$, $n = 6411$, $P < 0.001$) with the largest increases occurring when temperatures were coldest. Under these conditions, hares went from 0.35 min to 0.8 min of vigilance per min of activity. While the shape and magnitude of the responses to increasing wind speeds by hares were consistent between weather datasets, the temperature-dependence of the activity and vigilance responses were only present when using Haines Junction wind data (Supp. Figure S4.1).

In Canada lynx, average daily wind speed accounted for 1.6%, 1.8%, and 0.3% of the variance observed in daily activity, daily travel, and daily feeding events, respectively. However, lynx had the opposite response to wind as the prey species. Lynx increased daily activity and travel by ~ 2 h as daily wind speed increased (Fig. 2c; Activity: $F = 18.1$, $n = 1405$, $P < 0.001$; Travelling: $F = 19.2$, $n = 1405$, $P < 0.001$). Activity responses to daily wind were dependent on air temperature (Table S4.1; $F = 11.6$; $n = 1405$, $P < 0.001$) with stronger increases in activity with increasing wind when it was warmer out, while the response in daily travel to daily wind was temperature independent (Table S4.1). Lynx also increased the number of feeding events each day as daily wind speed increased (from 1.25 to 1.75 events between 0 and 25 km/hr) suggesting a potential improvement in foraging success (Fig. 2c; $F = 4.7$, $n = 1405$, $P = 0.03$). This increase in feeding was independent of air temperature (Table S4.1). While the direction and magnitude of the behavioural responses by lynx to wind were similar when analysis used ECMWF modelled wind speed data versus Haines Junction weather station data, the exact shape of the responses between no wind and high wind conditions changed from convex to concave depending on the wind dataset (Supp. Figure S4.1).

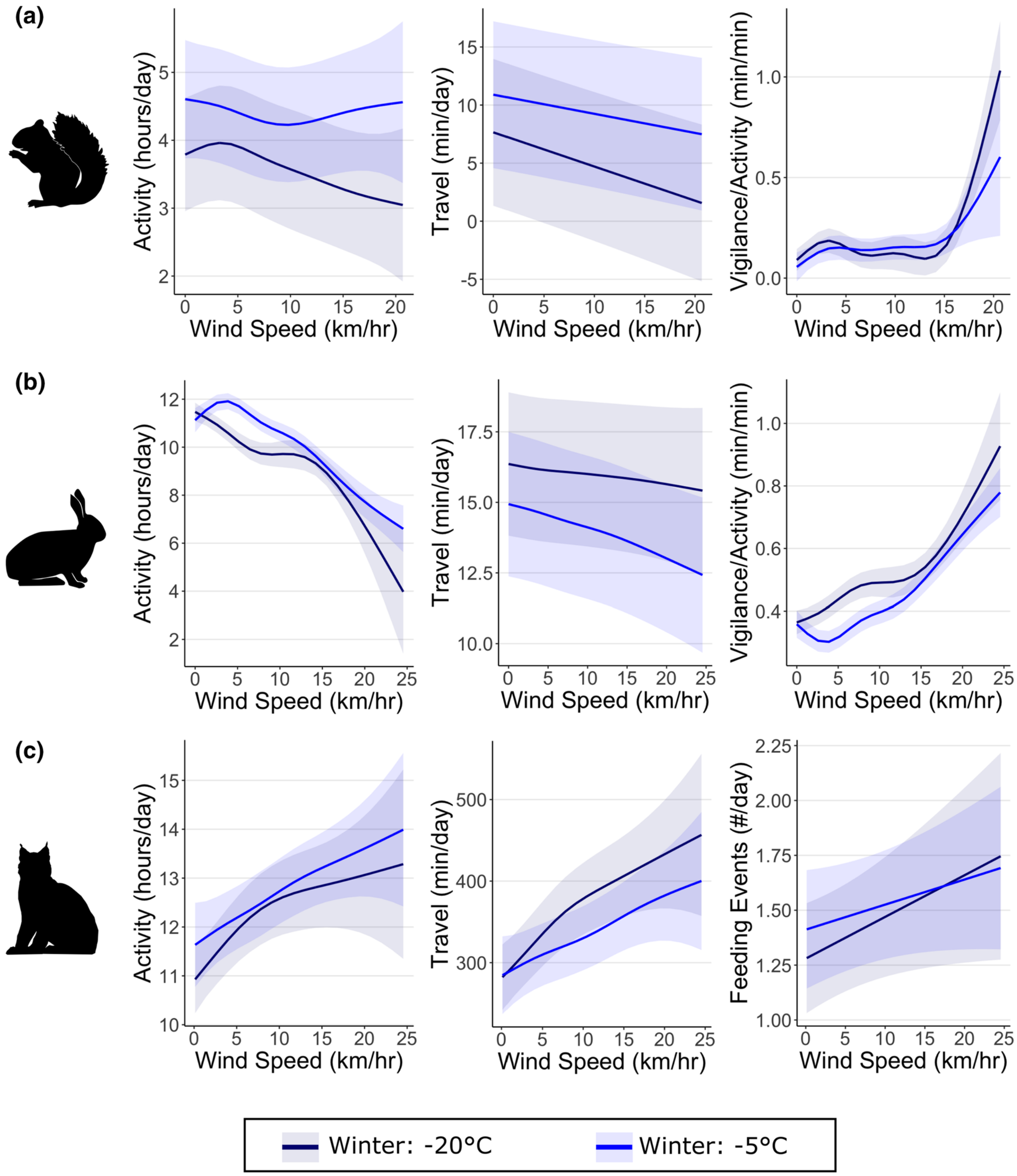

Fig. 2 Behavioural responses of red squirrels (**a**), snowshoe hares (**b**), and Canada lynx (**c**) to variation in average daily wind speed during winter. Modelled effects from global GAMM model for each species are shown for daily average air temperatures of – 20 ℃ (darker blue) and – 5 ℃ (lighter blue), although air temperature was a continuous variable in the model. Shading represents 95% confidence intervals

Discussion

We found correlative evidence that broad scale variation in daily wind speed can strongly influence the behaviour of terrestrial mammals living in forested environments. Snowshoe hares, red squirrels, and Canada lynx all made considerable adjustments (at least 25% change) to their daily activity and behaviour as daily wind speed increased. The daily activity response of red squirrels was only prominent at the coldest temperatures, while the responses of the other two species occurred regardless of air temperature. As lynx also increased their number of feeding events per day with increasing wind, there is evidence that wind may not only influence the behaviour of each species, but may also alter predator–prey dynamics in the boreal forest.

As this study is correlational, we acknowledge that we cannot confirm that the patterns we found here are caused by wind. However, with wind speeds varying at the scale of multiple days in winter when the landscape is frozen, wind becomes uncorrelated with many other environmental variables (e.g., solar radiation) that drive it during the rest of the year (Lensky et al. 2018). To increase our certainty that the responses by these boreal mammals are to wind and not some other environmental variable, we assessed the correlation between wind and other environmental variables (temperature, precipitation, and humidity) during the winter, and found that none varied with wind (all $R^2 < 0.2$). As there are no environmental variables that vary at the same temporal scale as winter wind patterns, we assume that the strong behavioural responses that we found in squirrels, hares, and lynx are reactions to changes in daily wind speed.

The magnitude of responses to wind that we observed here was substantial in hares and lynx relative to their responses to other environmental variables often considered strong influencers of behaviour. Snowshoe hares decreased daily activity by up to 8 h as daily wind speed increased from 0 to 20 km/hr, which is larger than the ~ 40 min activity reduction during a full moon (Studd et al. 2019a), and the ~ 15 min activity reduction after a close encounter with a predator (Shiratsuru et al. 2021). Lynx, which are relatively unresponsive behaviourally to environmental components like temperature (Menzies et al. 2022), increased daily activity by up to 2 h between weak and strong daily winds. While the behavioural responses in both species were strong in terms of the magnitude of change, there was considerable variation in lynx, suggesting that the responses were not universal in this species. This variation may be due to lynx behaviour like travel being conditional on behavioural motivators that tend to be more variable and less circadian in terrestrial mammalian predators than herbivores like time since last meal (e.g., hunger: Blecha et al. 2018; Aubier & Sherratt 2020) and hunting success (Říha et al. 2021). It is additionally important to note that while wind can drastically alter behaviour, it is in no way the only or most important thing influencing behaviour in these species as reflected in the relatively low amounts of overall variance explained by integrating wind into our models. This is unsurprising given that activity and behaviour are complex (Levitis et al. 2009; Baum 2013) outcomes of the optimization of energetic, survival, and reproductive gains (Shuter et al. 2012; Studd et al. 2020), which is influenced by a multitude of things like resource qualities and quantities (Burian et al. 2020), climate (e.g., Divoky et al. 2021), and predator numbers (e.g., Cunningham et al. 2019) that all naturally fluctuate over time. Thus, despite often being ignored, wind appears to be a critical component of forest environments that influences animal behaviour equally to, if not more than, other commonly considered abiotic conditions.

As wind can influence animals by altering either thermoregulation or sensory detectability, it is possible that each species may respond differently to wind depending on which consequence is more crucial. The opposing and relatively thermally independent responses that we observed by both predator and prey, in combination with the increased feeding events of the predator and the increased daily vigilance in the prey as daily wind speeds increased, suggest that the consequences of increased wind speeds for these forest-dwelling species are primarily due to effects that alter predator–prey detection (Jakosalem et al. 2013; Cherry & Barton 2017), and secondarily due to thermoregulation. This importance of wind consequences on predator–prey detection for these species aligns with our predictions that the forest provides shelter from wind at ground level (Davies-Colley et al. 2000) reducing the thermoregulatory effects, but the increased auditory and visual noise created by moving branches and structures within the canopy during strong winds (Yip et al. 2017) and the modified pathways of olfactory plumes by tree trunks (Fogarty et al. 2018) both alter signal detectability. Squirrels were the exception with a minimal response in daily activity to wind at warm temperatures and a large response at cold temperature, suggesting that their activity may be more controlled by thermoregulation (Mitchell et al. 2018) than predator detection. This may be due to their less thermally insulative fur coat and more arboreal nature which exposes them to higher thermal consequences and higher wind speeds than the other two ground-dwelling species (Pauls 1981; Moon et al. 2019). Additionally, the overall weaker response by squirrels than hares may also be due to the negative effects of wind on the flying and hunting abilities of avian predators (Quinn & Cresswell 2004).

While the behavioural adjustments by hares—reduced activity and increased vigilance—may help to increase detectability of predators in difficult conditions (Bowyer et al. 2001), lynx simultaneously increased their activity and likely hunting effort. Lynx increased the number of feeding events per day with stronger daily winds, suggesting that they may gain an advantage over hares under these conditions. As lynx primarily consume snowshoe hares in one meal (91.4% kills; Studd et al. 2021), and any cached food is consumed within a couple days of a kill (Studd unpublished), patterns seen in the number of daily feeding events are likely indicative of changes in kill rates. Thus, in addition to causing considerable behavioural responses in these forest-dwelling species, wind is also shaping the predator–prey interactions as seen in other systems (Stander & Albon 1993).

Given the magnitude of the behavioural responses we found that forest-dwelling animals have to wind, we believe that more consideration of this environmental component is needed in ecological studies, regardless of whether the habitat provides protection. Although the thermal constraints imposed by wind and how best to quantify them are often considered in thermoregulatory studies (Zerba et al. 1999; Porter 2016; Mitchell et al. 2018), the sensory constraints of wind are less commonly explored (although see Fairbanks & Dobson 2007; Carr & Lima 2010). This is likely because we often believe that an understanding of how wind affects detection requires measuring wind as experienced by the organism, which is multifaceted and often very localized; the effect changes depending on whether organisms are in or out of the wind, the direction of the wind, the frequency and strength of wind gusts, the differential noise generated by wind interacting with different surfaces in the local environment, and the redistribution of snow or debris by wind (including blowing substrate interfering with visual cues; Ruzicka & Conover 2011; Kogure et al. 2016; Cherry & Barton 2017). However, despite this complexity, we found strong behavioural responses to a very coarse measure of wind (average daily wind speeds as measured at a weather station). While each species is certainly responding to small-scale wind patterns, and finer detailed wind measurements in space and time may reveal additional, more subtle wind impacts and responses, we highlight that inclusion of wind at a course scale into behavioural analysis can be highly valuable and informative. Understanding how animals perceive and respond to wind, even in sheltered locations, will reveal important details of the control and maintenance of energetic balance, interspecies interactions, and ecological dynamics.

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Author contribution statement EKS, MJLP, and SB: conceived and designed the study; EKS, MJLP, YNM, AKM, RD, and JS: collected the data with support and input from all other authors; EKS: analyzed the data and led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

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Availability of data and materials All data used for this study are archived on Figshare https://doi.org/10.6084/m9.figshare.21119371.

Code availability All code is archived on Figshare https://doi.org/10.6084/m9.figshare.21119371.

Declarations

Conflict of interest Authors have no conflicts of interests.

Ethical approval All procedures were approved by animal care committee at University of Alberta (Protocol: AUP00001973) and/or McGill University (Protocol: 4728), and were conducted under Yukon Territorial Government Wildlife Research Permits and Scientist and Explorers Permits for each species and year.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Aubier TG, Sherratt TN (2020) State-dependent decision-making by predators and its consequences for mimicry. Am Nat 196(5):E127–E144

Barton BT (2014) Reduced wind strengthens top-down control of an insect herbivore. Ecology 95(9):2375–2381

Baum WM (2013) What counts as behavior? The molar multiscale view. The Behavior Analyst 36:283–293

Blecha KA, Boone RB, Alldredge MW, Kevin Blecha CA (2018) Hunger mediates apex predator's risk avoidance response in wildland-urban interface. J Anim Ecol. https://doi.org/10.1111/1365-2656.12801

Bowyer R, McCullough D, Belovsky G (2001) Causes and consequences of sociality in mule deer. Alces 37(2):371–402

Boyles JG, Bakken GS (2007) Seasonal changes and wind dependence of thermal conductance in dorsal fur from two small mammal species (*Peromyscus leucopus* and *Microtus pennsylvanicus*). J Therm Biol 32(7–8):383–387

Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. Adv Study Behav 35:151–209

Burian A, Nielsen JM, Winder M (2020) Food quantity–quality interactions and their impact on consumer behavior and trophic transfer. Ecol Monogr 90(1):e01395

Cáceres CE, Soluk DA (2002) Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408

Carr JM, Lima SL (2010) High wind speeds decrease the responsiveness of birds to potentially threatening moving stimuli. Anim Behav 80(2):215–220

Chen J, Franklin JF, Spies TA (1993) Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agric for Meteorol 63(3–4):219–237

Cherry MJ, Barton BT (2017) Effects of wind on predator-prey interactions. Food Webs 13:92–97

Conover MR (2007) Predator-prey dynamics: the role of olfaction. CRC Press, Boca Raton

Cunningham CX, Scoleri V, Johnson CN, Barmuta LA, Jones ME (2019) Temporal partitioning of activity: rising and falling top-predator abundance triggers community-wide shifts in diel activity. Ecography 42(12):2157–2168

Cuyler C, Øritsland NA (2002) Effect of wind on svalbard reindeer fur insulation. Rangifer 22(1):93

Dantzer B, Boutin S, Humphries MM, McAdam AG (2012) Behavioral responses of territorial red squirrels to natural and experimental variation in population density. Behav Ecol Sociobiol 66(6):865–878

Davies-Colley R, Payne G, van Elswijk M (2000) Microclimate gradients across a forest edge. N Z J Ecol 24(2):111–121

Divoky GJ, Brown E, Elliott KH (2021) Reduced seasonal sea ice and increased sea surface temperature change prey and foraging behaviour in an ice-obligate Arctic seabird, Mandt's black guillemot (Cepphus grylle mandtii). Polar Biol 44(4):701–715

Fairbanks B, Dobson FS (2007) Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. Anim Behav 73(1):115–123

Fogarty DT, Elmore RD, Fuhlendorf SD, Loss SR (2018) Variation and drivers of airflow patterns associated with olfactory concealment and habitat selection. Ecology 99(2):289–299

Graf RP, Sinclair ARE (1987) Parental care and adult aggression toward juvenile snowshoe hares. Arctic 40(3):175–178

Guillemette CU, Fletcher QE, Boutin S, Hodges RM, McAdam AG, Humphries MM (2009) Lactating red squirrels experiencing high heat load occupy less insulated nests. Biol Let 5(2):166–168

Hagemoen RIM, Reimers E (2002) Reindeer summer activity pattern in relation to weather and insect harassment. J Anim Ecol 71(5):883–892

Hayes AR, Huntly NJ (2005) Effects of wind on the behavior and call transmission of pikas (*Ochotona princeps*). J Mammal 86(5):974–981

Hollén LI, Bell MBV, Wade HM, Rose R, Russell A, Niven F, Radford AN (2011) Ecological conditions influence sentinel decisions. Anim Behav 82(6):1435–1441

Holt RD, Butler MJ (2019) Modeling audible detection of prairie grouse booming informs survey design. J Wildl Manag 83(3):638–645

Humphries MM, Boutin S, Thomas DW, Ryan JD, Selman C, McAdam AG, Speakman JR (2005) Expenditure freeze: the metabolic response of small mammals to cold environments. Ecol Lett 8(12):1326–1333

Jakosalem P, Collar NJ, Gill JA (2013) Habitat selection and conservation status of the endemic Ninox hawk-owl on Cebu, Philippines. Bird Cons Int 23:360–370

Kogure Y, Sato K, Watanuki Y, Wanless S, Daunt F (2016) European shags optimize their flight behavior according to wind conditions. J Exp Biol 219:311–318

Kolbe JA, Squires JR, Parker TW (2003) An effective box trap for capturing lynx. Wildl Soc Bull 31(4):980–985

Leihy RI, Chown SL (2020) Wind plays a major but not exclusive role in the prevalence of insect flight loss on remote islands. Proc R Soc B Biol Sci 287(1940):20202121. https://doi.org/10.1098/rspb.2020.2121

Lensky NG, Lensky IM, Peretz A, Gertman I, Tanny J, Assouline S (2018) Diurnal course of evaporation from the dead sea in summer: a distinct double peak induced by solar radiation and night sea breeze. Water Resour Res 54:150–160

Levitis DA, Lidicker WZ, Freund G (2009) Behavioural biologists do not agree on what constitutes behaviour. Anim Behav 78(1):103–110

Luther D, Gentry K (2013) Sources of background noise and their influence on vertebrate acoustic communication. Behaviour 150:1045–1068

McVicar TR, Roderick ML, Donohue RJ, Li LT, Van Niel TG, Thomas A, Dinpashoh Y (2012) Global review and synthesis of trends in observed terrestrial near-surface wind speeds: Implications for evaporation. J Hydrol 416–417:182–205

Menzies A, Studd E, Majchrzak Y, Peers M, Boutin S, Dantzer B, Humphries MM (2020) Body temperature, heart rate, and activity patterns of two boreal homeotherms in winter: homeostasis, allostasis, and ecological coexistence. Functl Ecol. https://doi.org/10.1111/1365-2435.13640

Menzies AK, Studd EK, Seguin JL, Derbyshire RE, Murray DL, Boutin S, Boutin S (2022) Activity, heart rate, and energy expenditure of a cold-climate mesocarnivore, the Canada lynx (*Lynx canadensis*). Can J Zool 100:261–272

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A (2018) Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. J Anim Ecol 87(4):956–973

Møller AP (2013) Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird. Ecosphere 4(1):art6

Moon K, Duff TJ, Tolhurst KG (2019) Sub-canopy forest winds: understanding wind profiles for fire behaviour simulation. Fire Saf J 105:320–329

Muñoz Sabater J (2019) ERA5-Land hourly data from 1981 to present. Copernicus climate change service (C3S) climate data store (CDS)

O'Donoghue M, Boutin S, Krebs CJ, Zuleta G, Murray DL, Hofer EJ (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79(4):1193–1208

Ord TJ, Peters RA, Clucas B, Stamps JA (2007) Lizards speed up visual displays in noisy motion habitats. Proc R Soc B 274:1057–1062

Pauls RW (1981) Energetics of the red squirrel: a laboratory study of the effects of temperature, seasonal acclimatization, use of the nest and exercise. J Thermal Biol 6:79–86

Peers MJL, Majchrzak YN, Menzies AK, Studd EK, Bastille-Rousseau G, Boonstra R, Boutin S (2020) Climate change increases predation risk for a keystone species of the boreal forest. Nat Clim Chang. https://doi.org/10.1038/s41558-020-00908-4

Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A, Krause BL, Napoletano BM, Pieretti N (2011) Soundscape ecology: the science of sound in the landscape. Bioscience 61(3):203–216

Porter W (2016) Heat balances in ecological contexts. In: Johnson EA, Martin YE (eds) A Biogeoscience approach to ecosystems. Cambridge University Press, Cambridge, pp 49–87

Quinn JL, Cresswell W (2004) Predator hunting behaviour and prey vulnerability. J Anim Ecol 73(1):143–154

Říha M, Gjelland KØ, Děd V, Eloranta AP, Rabaneda-Bueno R, Baktoft H, Peterka J (2021) Contrasting structural complexity differentiate hunting strategy in an ambush apex predator. Sci Rep 11(1):17472

Ruzicka RE, Conover MR (2011) Influence of wind and humidity on foraging behavior of olfactory mesopredators. Can Field-Nat 125(2):132

Shiratsuru S, Majchrzak YN, Peers MJL, Studd EK, Menzies AK, Derbyshire R, Boutin S (2021) Food availability and long-term predation risk interactively affect antipredator response. Ecology. https://doi.org/10.1002/ecy.3456

Shuter BJ, Finstad AG, Helland IP, Zweimü I, Hölker F (2012) The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat Sci 74:637–657

Stander P, Albon S (1993) Hunting success of lions in a semi-arid environment. Symp Zool Soc Lond 65:127–143

Studd EK, Boudreau MR, Majchrzak YN, Menzies AK, Peers MJL, Seguin JL, Humphries MM (2019a) Use of acceleration and acoustics to classify behavior, generate time budgets, and evaluate responses to moonlight in free-ranging snowshoe hares. Front Ecol Evol 7:154

Studd EK, Landry-Cuerrier M, Menzies AK, Boutin S, McAdam AG, Lane JE, Humphries MM (2019b) Behavioral classification of low-frequency acceleration and temperature data from a free-ranging small mammal. Ecol Evol 9:619–630

Studd EK, Menzies AK, Siracusa ER, Dantzer B, Lane JE, McAdam AG, Humphries MM (2020) Optimisation of energetic and reproductive gains explains behavioural responses to environmental variation across seasons and years. Ecol Lett 23:841–850

Studd EK, Derbyshire RE, Menzies AK, Simms JF, Humphries MM, Murray DL, Boutin S (2021) The Purr-fect Catch: using accelerometers and audio recorders to document kill rates and hunting behaviour of a small prey specialist. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.13605

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65(1):13–21

Togunov RR, Derocher AE, Lunn NJ (2017) Windscapes and olfactory foraging in a large carnivore. Sci Rep 7(1):46332

Vautard R, Cattiaux J, Yiou P, Thépaut J-N, Ciais P (2010) Northern hemisphere atmospheric stilling partly attributed to an increase in surface roughness. Nat Geosci 3(11):756–761

Velilla E, Muñoz M, Quiroga N, Symes L, ter Hofstede HM, Page RA, Halfwerk W (2020) Gone with the wind: Is signal timing in a neotropical katydid an adaptive response to variation in wind-induced vibratory noise? Behav Ecol Sociobiol 74(5):59

Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc R Soc B 267:1869–1874

Weimerskirch H, Louzao M, de Grissac S, Delord K (2012) Changes in wind pattern alter albatross distribution and life-history traits. Science 335(6065):211–214

Wood S (2017) generalized additive models: an introduction with R, 2nd edn. CRC Press, Chapman and Hall

Yip DA, Bayne EM, Campbell J, Proppe D (2017) Sound attenuation in forest and roadside environments: implications for avian point-count surveys. Condor 119:73–84. https://doi.org/10.1650/CONDOR-16-93.1

Zerba E, Dana AN, Lucia MA (1999) The influence of wind and locomotor activity on surface temperature and energy expenditure of the Eastern House Finch (*Carpodacus mexicanus*) during cold stress. Physiol Biochem Zool 72(3):265–276