1   # Temperature shapes movement and habitat selection by a heat-

2   # sensitive ungulate

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Abstract

1. Warmer weather caused by climate change poses increasingly grave threats to the persistence of many species, but animals can modify behavior to mitigate at least some of the threats posed by warmer temperatures. Identifying and characterizing how animals behaviorally thermoregulate to avoid the negative consequences of acute heat will be crucial for predicting animal responses to a warmer future.

2. We used a step-selection function to reveal whether moose (*Alces alces*), a species known to be sensitive to heat, mitigate heat via reduced movement, increased visitation to shade, or increased visitation to water on hot summer days in northeastern Minnesota, USA.

3. Moose reduced movement, sought shade, and traveled nearer to mixed forests and bogs during periods of heat. Moose used shade far more than water to ameliorate heat, and the most pronounced changes in behavior occurred between 15˚C and 20˚C.

4. When temperatures are high, moose face tradeoffs between foraging and keeping cool. Forgoing foraging to avoid overheating may have contributed to recent population declines in our study area and other areas across the southern edge of moose distribution.

5. Research characterizing the behaviors animals use to facilitate thermoregulation and the consequences of those behaviors for fitness will aid conservation of heat-sensitive species in a warming world. Step-selection functions are a promising tool for such analyses.

Key-words climate change, habitat selection, habitat use, lidar, moose (*Alces alces*), resource selection, step-selection function, thermal refugia

1. Introduction

Animal performance peaks within a limited range of body temperatures in which molecular, cellular, and systemic processes operate optimally. Body temperatures outside this range impose functional constraints on these processes, including reductions in growth, reproduction, activity, and immune function (Pörtner & Farrell, 2008). Nevertheless, animals routinely operate in environmental conditions that trigger suboptimal body temperatures (Boyles, Seebacher, Smit, & McKechnie, 2011; Sunday et al., 2014). This conundrum underlies two long-standing questions in biological research: (1) How can animals mitigate suboptimal thermal conditions, and (2) how effective are those efforts at mitigation? Rapid and ongoing responses to global climate change by a multitude of animal species (Hoegh-Guldberg & Bruno, 2010; Parmesan, 2006; Walther et al., 2002) increase the urgency of answering those questions.

Animals can loosen the constraints of limited ranges of thermal tolerance by adjusting their behavior to facilitate thermoregulation. Such behavioral thermoregulation has a long history of study in biological research (Cowles & Bogert, 1944), but this idea still offers fresh insight today. Animals can restrict movement to produce less metabolic heat (Broders, Coombs, & McCarron, 2012; Stelzner, 1988), alter posture to reduce heat gain from insolation or increase surface area to shed heat (Bartholomew & Dawson, 1979; Luskick, Battersby, & Kelty, 1978), pant to lose heat via evaporation (Campos & Fedigan, 2009; McCann, Moen, & Harris, 2013), or visit thermal refugia (spaces that provide refuge from thermal stress caused by extreme temperatures [e.g., burrows, wallows, shade cover]; Hovick, Elmore, Allred, Fuhlendorf, & Dahlgren, 2014; Kurylyk, MacQuarrie, Linnansaari, Cunjak, & Curry, 2015; van Beest, Van Moorter, & Milner, 2012), among other behaviors. Identifying exactly which of these strategies animals use to behaviorally thermoregulate, how much these strategies buffer against adverse

63 impacts of hot weather, and what costs animals incur to use these strategies is crucial for

64 understanding their ability to increase ranges of thermal tolerance.

65   Recent advances in statistical modeling techniques provide opportunity to study

66 behavioral thermoregulation in new ways. Step-selection functions (hereafter "SSFs") are a

67 relatively recent extension of the resource selection function modeling framework that explicitly

68 incorporates spatial and temporal animal movement characteristics to enable examination of

69 fine-scale habitat selection and movement behavior at biologically realistic scales (Duchesne,

70 Fortin, & Rivest, 2015; Forester, Im, & Rathouz, 2009; Thurfjell, Ciuti, & Boyce, 2014). SSFs

71 have primarily been used to model habitat selection (Thurfjell et al., 2014), but recent theoretical

72 development has demonstrated that they can also be used to explicitly model movement behavior

73 that changes in both space and time in relation to landscape features (Avgar, Potts, Lewis, &

74 Boyce, 2016; Ladle et al., 2019; Prokopenko, Boyce, & Avgar, 2017). By including interaction

75 terms between temperature, habitat covariates, and movement rates within SSFs, temperature-

76 dependent animal behaviors—including both resource selection and movement rates—can be

77 explicitly quantified.

78   We evaluated behavioral thermoregulation using the SSF framework in moose (*Alces*

79 *alces*), a well-known heat-sensitive species. Moose have undergone substantial population

80 declines across much of their southern range due in part to climate change (Lenarz, Nelson,

81 Schrage, & Edwards, 2009; Monteith et al., 2015; Rempel, 2011). Moose experience heat stress

82 starting at temperatures as low as 14˚C (Renecker & Hudson, 1986) or 17˚C (McCann et al.,

83 2013) during the summer. Moose prevent heat stress on hot days by using water, shade, and

84 decreased activity to shed heat via conduction and reduced exposure to radiation from the sun

85 (Belovsky, 1981; Broders et al., 2012; Dussault et al., 2004; McCann, Moen, Windels, & Harris,

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86   2016; Street, Rodgers, & Fryxell, 2015). At coarse spatial and temporal scales, moose select for

87   thermal cover (e.g., dense canopy in conifer forests) during periods of high temperatures

88   (Demarchi & Bunnell, 1995; Melin et al., 2014; Schwab & Pitt, 1991; Street et al., 2016; van

89   Beest et al., 2012; but see Lowe, Patterson, & Schaefer, 2010). However, earlier studies have not

90   established the relative importance of multiple different heat amelioration strategies (e.g.,

91   seeking shade vs. reducing movement vs. visiting water) or identified thresholds at which moose

92   behavioral thermoregulation alters habitat selection.

93   To evaluate how moose modify fine-scale habitat selection and movement patterns as

94   temperatures increase, we used an SSF to assess effects of temperature on movement and

95   resource selection. We examined empirical support for a single model consisting of temperature

96   and interactions with variables likely to be important for moose thermoregulation. This model

97   enabled us to test three hypotheses on how moose alter behavior to thermoregulate when it is hot:

98   (1) moose decrease movement rates to decrease metabolic heat production, (2) moose increase

99   use of shade to decrease heat gain from solar radiation, or (3) increase use of water to increase

100   heat loss via conduction, convection, and evaporation.

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102   **2. Materials and Methods**

103   **2.1 Study area.**

104   We conducted our study in northeastern Minnesota, USA (Fig. 1). Federal, state, county,

105   and tribal public lands managed for timber harvest and recreation make up >80% of property

106   ownership in the area. The region is a sub-boreal transition zone between northern hardwood

107   forests in the south to Canadian boreal forests in the north (Pastor & Mladenoff, 1992). Upland

108   forests are primarily composed of white, red, and jack pine (*Pinus strobus*, *P. resinosa*, and *P.*

109   *banksiana*), aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and balsam fir (*Abies*

110   *balsamea*). Black spruce (*Picea mariana*), tamarack (*Larix laricina*), and northern white cedar

111   (*Thuja occidentalis*) dominate wet lowland forests. Mean minimum and maximum temperatures,

112   respectively, are -16.5˚C and -5.5˚C for the month of January and 12.6˚C and 24.0˚C for the

113   month of July at the Beaver Bay weather station on the southern edge of our study area (National

114   Oceanic and Atmospheric Administration). Snow cover is typically present from December to

115   April, with mean annual snowfall ranging between 150 – 240 cm (Minnesota Department of

116   Natural Resources).

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118   **2.2 Animal Capture and GPS Telemetry**

119   We captured moose by darting them from helicopters (Quicksilver Air, Inc., Fairbanks,

120   Alaska, USA) during the winters of 2011 and 2012. Darts used to sedate moose contained 1.2 ml

121   (4.0 mg ml^{-1}) carfentanil citrate and 1.2 ml (100 mg ml^{-1}) xylazine HCl, and we used 7.2 ml (50

122   mg ml^{-1}) naltrexone HCl and 3 ml (5 mg ml^{-1}) yohimbine HCl as antagonists (Lenarz et al.,

123   2009; Roffe, Coffin, & Berger, 2001). We fitted immobilized moose with global positioning

124   system (GPS) collars (Lotek Wireless, Inc., Newmarket, Ontario, Canada). Animal capture and

125   handling protocols met American Society of Mammalogists recommended guidelines (Sikes &

126   Animal Care and Use Committee of the American Society of Mammalogists, 2011) and were

127   approved by the University of Minnesota Animal Care and Use Committee (Protocol Number:

128   1309-30915A).

129   Collars were programmed to record locations every 20 minutes and to drop off moose at

130   the end of expected battery life (2 years). We retained GPS locations with 3-D fixes or 2-D fixes

131   with dilution of precision values ≤ 5 (Lewis, Rachlow, Garton, & Vierling, 2007) and removed

132   locations that were not biologically possible (i.e., removing locations where the distance between

133   locations would have exceeded the distance a moose could have moved in a 20-minute period,

134   assuming a maximum speed of 30-km/hour). Data used in this analysis include only locations

135   between May 1 and September 31—dates that coincide with average daily maximum

136   temperatures above the threshold believed to induce heat stress for moose (Renecker & Hudson,

137   1986). Location and activity data within 2 weeks of death or collar failure were censored from

138   our data, and only full months of data were used in analysis. One hundred fifty-three moose-

139   months of 24 moose were used in final analysis.

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141   **2.3 Model Covariates**

142   Because shade is difficult to directly calculate over large areas at fine scales and varies at

143   any given location on daily and annual cycles, we used canopy vegetation density as a proxy for

144   shade. Canopy vegetation density was estimated using airborne lidar data. Lidar is an active,

145   laser-based remote sensing technology that provides detailed information on topography and

146   vegetation structure (Davies & Asner, 2014; Vierling, Vierling, Gould, Martinuzzi, & Clawges,

147   2008). Lidar data were collected over our entire study area during leaf-off conditions in May

148   2011 as part of the Minnesota Elevation Mapping project (Minnesota Geospatial Information

149   Office). Lidar data were collected from a fixed wing airplane at an altitude of 2,000-2,300 m

150   above ground level using discrete-return laser scanning systems (ALS60, ALS70, or Optech

151   GEMINI). Side overlap was 25% with a scan angle of $\pm$ 20°. Nominal point spacing and pulse

152   density varied due to incomplete overlap of adjacent flight-lines. Average nominal pulse density

153   was 1 pulse/m^2. We calculated height of discrete returns above ground by subtracting ground

154   elevation based on a lidar-derived Digital Elevation Model from the return elevation. Lidar data

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155   met National Standard for Spatial Database Accuracy standards and had a vertical accuracy

156   RMSE of 5.0 cm and a horizontal accuracy of 1.16 m.

157   We estimated canopy vegetation density as the proportion of all returns that were ≥ 3 m

158   above ground. Lidar-derived canopy vegetation density estimates were summarized in a 30 x 30

159   m grid that aligned with National Land Cover Database (NLCD) raster data to ensure

160   consistency across data layers in GIS. We used FUSION software to create the lidar-derived

161   canopy vegetation density raster (McGaughey, 2016). For the sake of simplicity, we hereafter

162   refer to canopy vegetation density as "shade".

163   Land cover types were determined using the 2011 National Land Cover Database

164   (NLCD) (Homer et al., 2015). NLCD is a remotely sensed dataset of 16 land cover classes

165   created from Landsat Thematic Mapper with 30 m spatial resolution. We extracted 5 vegetation

166   cover types that may offer thermal refuge—woody wetland, hereafter called bog; emergent

167   herbaceous wetland, hereafter called marsh; open water; conifer forests; and mixed forests. Each

168   of these cover types offers different amounts of thermal refuge via different mechanisms (Table

169   1). Each cover type also offers different amounts of forage. Since moose primarily eat the leaves

170   of deciduous shrubs and saplings < 3 m tall during summer, forage quantity decreases as the

171   amount of shade and proportion of conifers increases. We calculated the distance of each pixel in

172   our study area from each of our chosen land cover types using ArcMap 10.4 (Esri, Redlands,

173   California, USA).

174   Temperature data used to define our study period were obtained from two weather

175   stations within our study area (KBFW in Silver Bay and KCKC in Grand Marais; MesoWest),

176   which report temperatures at 20-minute intervals. Moose locations were individually matched

177   with the nearest weather station (by distance) and nearest temperature recording (by time).

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178   Moose locations were on average 33 km from the nearest weather station and 7 mins from the

179   closest recorded weather observation in time.

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181   **2.4 Statistical Analysis**

182   We used a step-selection function (SSF) to model moose resource selection and

183   movement behavior. For our SSF, we selected available points using a parameterized Weibull

184   distribution of step lengths and the observed distribution of turn angles of the animals in our data

185   set. We paired 20 available locations to each used location (i.e., 21 points per stratum). Our final

186   data set contained 311,521 steps taken by 24 moose. We used conditional logistic regression to

187   fit the SSF containing our variables of interest (listed in Table 1) and interactions between each

188   variable and ambient temperature. We included step length (i.e., distance between consecutive

189   fixes) both to reduce bias in selection estimates (Forester et al., 2009) and to explicitly model its

190   interaction with another variable of interest (Avgar et al., 2016; Ladle et al., 2019; Prokopenko et

191   al., 2017). Interaction coefficients detail how temperature influences step length and selection of

192   cover types at differing temperatures. Because step lengths vary in a regular pattern over the

193   course of each 24-hour period (Fig. A1), we adjusted step lengths prior to inclusion in the model

194   by subtracting the observed step length from the average step length at each given time of day.

195   Failure to adjust for crepuscular activity peaks could lead to consistent positive bias in movement

196   rates at low (morning) and intermediate (evening) temperatures. We included one-way

197   interactions between each covariate and temperature (˚C). Because temperature was constant

198   within strata, it was considered only as an interaction term. The full final model is listed below:

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200   Use ~ Shade + dBog + dMarsh + dWater + dConifer + dMixed + StepLength + Temp*Shade +

201   Temp*dBog + Temp*dMarsh + Temp*dWater + Temp*dConifer + Temp*dMixed +

202   Temp*StepLength,

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204   where "*" denotes interactions between variables. We used generalized estimating equations

205   (GEEs) to obtain robust standard errors among animal-days that reduce Type I error caused by

206   pseudoreplication (Craiu, Duchesne, & Fortin, 2008; Duchesne, Fortin, & Courbin, 2010; Fortin

207   et al., 2005), and checked to ensure that VIFs between main effects were adequately low

208   (Dormann et al., 2013). We then conducted k-fold (k=5) cross-validation on our final model and

209   calculated Spearman rank correlation (mean of 50 replications) to evaluate model fit (based on

210   the methods of Fortin et al., 2009). Finally, we rarified data to 1-, 2-, and 4-hour intervals to

211   determine the minimum interval between GPS locations required to detect biologically

212   significant interactions. All analyses were conducted using R statistical software (R Core Team,

213   2018).

214

215   **3. Results**

216   **3.1 Moose Movement and Resource Selection**

217   We found empirical support for four interaction terms (StepLength*Temp, Shade*Temp,

218   Bog*Temp, MixedForest*Temp) in our step-selection function (Table 2), indicating that

219   temperature significantly altered movement rate and selection for shade, bog, and mixed forest.

220   We did not detect empirical support for interactions between temperature and distance to marsh,

221   temperature and distance to open water, or temperature and distance to conifer forest. Of these

222   variables with interaction terms whose 95% CIs overlapped zero, only the main effect for

223 distance to conifer forest was significant. Regardless of temperature, moose selected areas

224 further from conifer forest (RSS = 1.553; 95% CI = 1.133-2.130). The main effects for distance

225 to marsh and distance to open water were not significant. Moose neither selected nor avoided

226 areas near marsh or open water.

227 Moose decreased movement rates at hotter temperatures (Fig. 2A). Mean standardized

228 step length was below 0 m at all temperatures above 20˚C. In other words, the mean step length

229 at each temperature above 20˚C was below the overall mean step length (controlling for time of

230 day). At each standardized step length > 0 m (i.e., steps that were longer than average), the odds

231 of moose taking a step of that length was higher at 0˚C than at 15˚C, and higher at 15˚C than at

232 30˚C. At 0˚C, the odds that moose would move 100 m more than average in 20 minutes were

233 substantially higher (RSS = 1.074; 95% CI = 1.025-1.126) than at 15˚C (RSS = 0.849; 95% CI =

234 0.777-0.928), which were in turn substantially higher than at 30˚C (RSS = 0.672; 95% CI =

235 0.590-0.765).

236 Moose spent more time in shade at hotter temperatures (Fig. 2B). Relative selection

237 strength increased with increasing vegetative cover at 30˚C, while it decreased with increasing

238 vegetative cover at 0˚C and 15˚C, indicating that moose sought shade at high temperatures while

239 avoiding it at lower temperatures. At 0˚C, the odds that moose would move into a pixel with

240 75% vegetative cover were substantially lower (RSS = 0.265; 95% CI = 0.239-0.295) than at

241 15˚C (RSS = 0.640; 95% CI = 0.523-0.782), which were in turn substantially lower than at 30˚C

242 (RSS = 1.542; 95% CI = 1.148-2.073).

243 Despite avoiding bogs at colder temperatures, moose traveled closer to bogs at hotter

244 temperatures (Fig. 2C). The odds that moose were far from bogs was higher at 0˚C (RSS =

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245   1.407; 95% CI = 1.177-1.681 at 500 m) than at 15˚C (RSS = 0.818; 95% CI = 0.577-1.160 at 500

246   m), and higher at 15˚C than at 30˚C (RSS = 0.476; 95% CI = 0.283-0.800 at 500 m).

247   Moose selected for shorter distances to mixed forest when it was hot than when it was

248   cold (Fig. 2D). The odds that moose were far from mixed forest was higher at 0˚C (RSS = 1.064;

249   95% CI = 0.888-1.274 at 500 m) than at 15˚C (RSS = 0.795; 95% CI = 0.560-1.127 at 500 m) or

250   30˚C (RSS = 0.594; 95% CI = 0.353-0.998 at 500 m), though odds did not significantly differ

251   between 15˚C and 30˚C.

252

253   **3.2 Model validation**

254   K-fold cross-validation of our model demonstrated that our model was substantially better than

255   random at predicting where moose moved—the mean Spearman rank correlation coefficient was

256   0.47 for observed steps.

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258   **3.3 Effects of temporal scale on interactions**

259   The interactions we found in our data diminish substantially if GPS locations are rarified so that

260   locations occur at longer intervals. If our 20-min GPS data are rarified to 1-hr, 2-hr, and 4-hr

261   intervals and used to fit the same SSF, interactions become progressively less biologically

262   meaningful (Fig. A2). As the intervals increase, differences across temperatures for step length,

263   shade, and distance to bog become minimal. Differences across temperatures for distance to

264   mixed forest shrink, but more gradually. This pattern of weakening interactions as intervals

265   between GPS locations increase indicates that fine-scale data may be required to detect

266   behavioral mitigation strategies by moose using step-selection functions.

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4. Discussion

Moose altered both movement and habitat selection to behaviorally thermoregulate during hot periods. Moose reduced movement and increased use of shade, bogs, and mixed forest at high heat, even while avoiding shade and bogs at cooler temperatures (Fig. 2). This pattern links previous findings of separate studies. First, moose prefer to forage in areas with low canopy cover because canopy cover is generally inversely related to forage availability (Lone et al., 2014). Second, moose prefer to use bed sites under dense forest canopy in wet lowland forests during the day (McCann et al., 2016), where moose have access to less forage but more protection against heat gain from solar radiation and more capacity to lose heat to the ground via conduction. Moose therefore face a steep tradeoff during periods of heat—areas that are good for foraging are not good for avoiding heat. Selection for shade and shorter step lengths as temperatures increase indicates that moose forego foraging in favor of bedding down under shade as temperatures increase. Earlier studies have documented moose shifting activity to cooler evenings and nights on hot days (Dussault et al., 2004; Montgomery et al., 2019), which is consistent with this trade-off.

The vegetation cover types used more by moose during warm weather further indicate that moose face a tradeoff between foraging and thermoregulation during periods of heat. In general, moose are more likely to find greater quantities of forage in cover types that do not provide thermal cover, while cover types that provide thermal cover are less likely to provide forage. For example, upland mixed forest has some available forage, but forage availability is highest in this cover type in young forests with little canopy cover. Similarly, bogs in Minnesota are largely populated by black spruce, tamarack, and alder, all of which can provide thermal cover but are unpalatable for moose. Birch (*Betula* spp.) and willow (*Salix* spp.) are more

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291   palatable and occasionally grow in bogs in Minnesota, but rarely at densities high enough to

292   compensate for unpalatable species dominating the canopy layer.

293   During hot weather, moose used shade far more than water to ameliorate heat. Moose are

294   commonly observed in bodies of water, and anecdotal evidence suggests that moose use water to

295   shed heat (Demarchi & Bunnell, 1995; Schwab & Pitt, 1991). Our analysis, however, indicates

296   that moose do not often use open water and marsh to mitigate heat stress; they prefer to seek

297   shadier land cover types. Nevertheless, they do increase use of woody bogs—where both shade

298   and some water are usually available—as temperatures increase. This is consistent with a

299   previous study (McCann et al., 2016) that found that moose prefer bed sites with both canopy

300   cover and relatively high soil moisture.

301   Frequent GPS locations enabled us to detect this pattern and may explain why previous

302   attempts to characterize moose movement patterns failed to reveal a clean relationship between

303   temperature and movement rates (Dussault et al., 2004; Montgomery et al., 2019). Moose spend

304   about half of their day foraging during the summer, with foraging bouts interspersed by periods

305   of rumination at bed sites. Periods of rest and rumination are typically distinct and occur at

306   regular intervals of roughly 2 hours (Moen, Pastor, Cohen, & Schwartz, 1996; Renecker &

307   Hudson, 1989). As the interval between GPS locations increases, the chance that both

308   ambulatory foraging bouts and stationary ruminating bouts are aggregated into a single GPS fix

309   increases, which homogenizes step lengths (Moen et al., 1996). Frequent GPS locations reduce

310   the probability of this happening. Indeed, if our location data is rarified to 1-, 2-, and 4-hour

311   intervals, interactions between temperature and movement rates are progressively reduced (Fig.

312   A2). Because many species have idiosyncratic movement behaviors, movement studies may

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313   require intervals between GPS locations within a specific range to answer some research

314   questions.

315   Our analysis can directly inform management and conservation actions for wildlife.

316   Moose populations at the southern edge of their distribution (including our study area) have

317   undergone dramatic declines in the past decade. Our results suggest that in a warmer future

318   proximity to shade will strongly influence habitat suitability for moose in areas with abundant

319   forage due to timber harvest and other anthropogenic disturbance. Moose will likely benefit from

320   management action to explicitly promote maintenance of shade near large patches of forage.

321   Because moose prioritize shade over forage when it is hot, moose will likely not feed in large

322   forest openings on hot days (though moose may feed in unshaded forest openings at night

323   [Dussault et al., 2004]). Moose will likely spend more time foraging in forest openings with

324   patches of canopy cover than in large homogeneous forest openings. For example, most of the

325   forage in large clearcuts may be inaccessible to moose during hot periods unless the clearcuts

326   contain "reserve patches", or interior islands or fingers of forest extending into the clearcut.

327   These reserve patches will likely be most helpful for moose if they consist of bog or mixed

328   forest.

329   Because we did not measure fitness or any proxy for it, it remains unclear how effective

330   these behavioral strategies will be at reducing population declines under climate change.

331   Although behavioral thermoregulation mitigates some metabolic costs of hot weather, forgoing

332   foraging to avoid high body temperatures may result in decreased fat reserves, lower fitness, and

333   ultimately in population declines compared to a cooler baseline scenario where moose do not

334   need to behaviorally thermoregulate. However, identifying patterns of behavior allows

335   researchers to explicitly test for fitness consequences in subsequent studies. For example,

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336   identification of "green wave surfing" behavior (by which animals migrate along paths of rapidly

337   greening forage) in migratory ungulates (Aikens et al., 2017; Merkle et al., 2016) allowed

338   researchers to later show that better green wave surfers had higher body fat and increased

339   reproductive success (Middleton et al., 2018). Our study could be used as a foundation for

340   further analyses along these lines, or to parameterize mechanistic models of moose energetic

341   balances under various climate scenarios, land management strategies, or disturbance regimes to

342   project the outcomes of conservation actions taken to benefit moose. Future studies should

343   characterize fitness consequences associated with reduced movement and increased time spent in

344   areas with low forage availability during warm periods.

345   Our analysis demonstrates that advances in animal tracking, remote sensing, and

346   modelling techniques allow us to study responses by free-ranging animals to weather in the field

347   at finer scales than previously possible. SSFs in particular are a valuable tool to answer questions

348   concerning behavioral responses by free-ranging animals to changes in weather in a relatively

349   simple and intuitive way. Because SSFs estimate selection conditionally at each GPS location,

350   each location or step can be connected with a distinct time and spatial location, enabling

351   inference on how animals change movement and habitat selection behavior in space and time in

352   response to specific stimuli. SSFs have been used to characterize animal movements in relation

353   to landscape features, such as grizzly bear response to human activity (Ladle et al., 2019) and elk

354   and African wild dog response to roads (Abrahms et al., 2016; Prokopenko et al., 2017).

355   Likewise, SSFs can characterize changes in movement behavior and habitat use in response to

356   differences in temperature. Similar analyses will be increasingly important on a warming planet,

357   and continued advances in animal tracking and remote sensing technologies will allow us to

358   study such behavior at finer scales and for many more species than have been studied in the past.

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359   In conclusion, moose altered both movement and habitat selection to behaviorally

360   thermoregulate during hot periods by reducing movement rates and increasing use of shaded

361   vegetation cover types that they avoid at cooler temperatures. Moose did not regularly use water

362   sources that lack canopy cover to shed heat. Moose face a tradeoff between forage and thermal

363   cover at high temperatures and forego foraging in favor of seeking thermal cover. Behavior

364   changed at thresholds near (though somewhat above) previously documented heat stress

365   thresholds (McCann et al., 2013; Renecker & Hudson, 1986): step lengths decreased at

366   temperatures above 20˚C, and selection patterns for shade cover reversed above 15˚C. Future

367   research characterizing strategies for behavioral thermoregulation and consequences of those

368   strategies for fitness will aid conservation in a warming world, for both moose and other heat-

369   sensitive species.

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Author Contributions

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381   JA and RM conceived and designed the study; RM collected the data; JA, MJ, and JM analysed

382   the data; JA led the writing of the manuscript. All authors contributed critically to manuscript

383   drafts and gave final approval for publication.

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Data Availability

386   Data and R scripts will be archived on *Zenodo* when this manuscript is accepted for publication.

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Figures

571   Fig. 1. The physical characteristics of the surrounding environment greatly influence the thermal landscape for animals. Fig. 1A

572   represents an environment (conifer forest) where heat gain may be decreased by reducing exposure to radiation, Fig. 1B represents an

573   environment (marsh) where heat loss may be increased by conduction, and Fig. 1C represents an environment (clear cut) that offers

574   neither relief from radiation nor opportunities to disperse heat via conduction. Moose likely face tradeoffs between forage availability

575   and thermal relief.
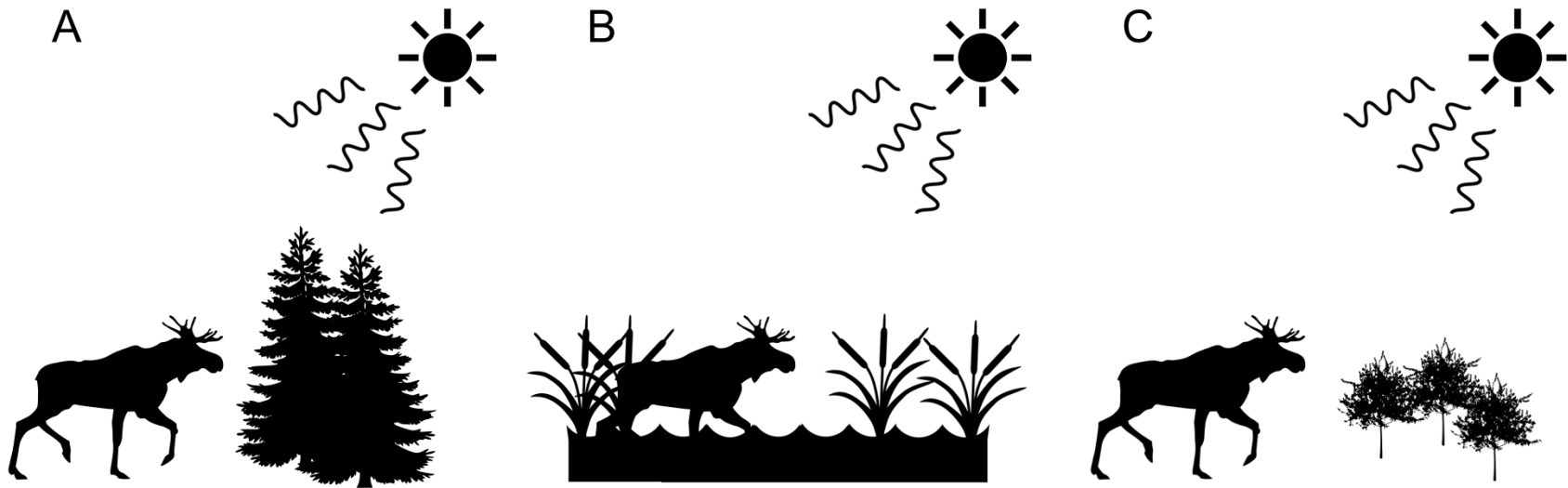
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578   Fig. 2. Interaction plots showing relationships for significant interactions between temperature and relative selection strengths (RSS)

579   of variables of interest (A: Step length and temperature, B: Shade and temperature, C: Distance to bog and temperature, D: Distance to

580   mixed forest and temperature). High temperatures decrease the odds of longer step lengths, increase the odds of seeking shade, and

581   increase the odds of traveling in bogs and mixed forest. In some cases (A, B, and C), patterns of behavior at low temperatures reversed

582   into patterns of the opposite behavior at high temperatures (e.g., moose strongly avoid shade at 0˚C while strongly selecting for shade

583   at 30˚C).

584
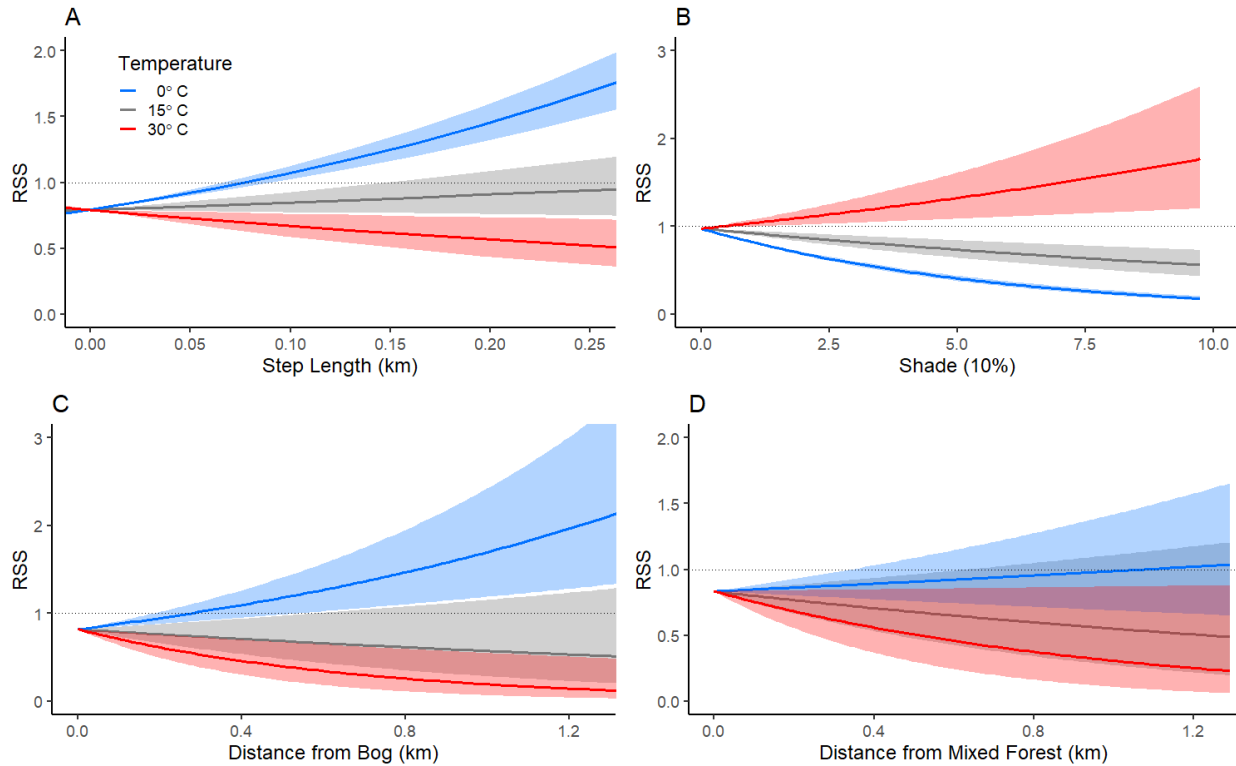
Tables

586 Table 1. Variables incorporated in the step-selection function of moose movement and habitat selection and justification for inclusion

587 in the model.

Name	Variable	Description
Shade	Canopy Vegetation Density	Proportion of all lidar returns above 3 meters; analogous to canopy vegetation density, a proxy for shade
dBog	Distance to Bog	Distance to woody wetlands; included in analyses because bogs have both canopy cover and ground moisture
dMarsh	Distance to Marsh	Distance to emergent herbaceous wetlands; included in analyses because moose are often observed in marshes, and water can disperse heat via conduction, convection, and evaporation
dWater	Distance to Open Water	Distance to open water; included in analyses because moose are often seen in bodies of water, which can disperse heat via conduction, convection, and evaporation
dConifer	Distance to Conifer Forest	Distance to conifer forest; included in analyses because conifer forest contains localized thick canopy cover
dMixed	Distance to Mixed Forest	Distance to mixed forest; included in analyses because conifers offer localized thick canopy cover while deciduous trees offer foraging opportunities
StepLength	Step Length	Distance between a moose location and the location immediately prior; included in analyses to account for bias in the parametric distribution of step lengths used to characterize available points and to estimate how temperature affects movement rates
Temp	Temperature	Temperature at the nearest NOAA weather station at the time of a location; included in analyses to estimate how temperature affects habitat use and movement rates

Table 2. Coefficient estimates, standard errors, relative selection strengths, 95% confidence intervals, and p-values for the step-selection function. Bold variables denote significance at α = 0.05.

Variable	Coefficient	Robust SE	RSS	RSS LCL	RSS UCL	p
Shade	**-0.174**	**0.007**	**0.840**	**0.829**	**0.852**	**<0.001**
dBog	**0.728**	**0.182**	**2.071**	**1.450**	**2.956**	**<0.001**
dMarsh	-0.055	0.108	0.947	0.767	1.169	0.612
dWater	0.057	0.106	1.058	0.860	1.302	0.592
dConifer	**0.440**	**0.161**	**1.553**	**1.133**	**2.130**	**0.006**
dMixed	0.169	0.184	1.184	0.825	1.699	0.359
StepLength	**3.025**	**0.242**	**20.603**	**12.831**	**33.082**	**<0.001**
Shade*Temp	**0.008**	**0.000**	**1.008**	**1.007**	**1.009**	**<0.001**
dBog*Temp	**-0.072**	**0.012**	**0.930**	**0.909**	**0.952**	**<0.001**
dMarsh*Temp	0.004	0.007	1.004	0.990	1.019	0.558
dWater*Temp	-0.004	0.007	0.996	0.982	1.010	0.589
dConifer*Temp	-0.009	0.010	0.991	0.972	1.011	0.388
dMixed*Temp	**-0.039**	**0.012**	**0.962**	**0.940**	**0.984**	**0.001**
StepLength*Temp	**-0.156**	**0.014**	**0.855**	**0.832**	**0.879**	**<0.001**

Appendix A: Supplementary Data

Fig. A1. Lowess regression of mean step length across times of day (20 min. increments). The gray ribbon represents the 95% confidence interval for the regression line. Moose movement rates varied slightly but consistently over the course of the day, with movement rates peaking during crepuscular periods. The area within the dotted rectangles represents the range of civil sunrise and sunset at the centroid of our study area during our study period (determined using the NOAA Solar Calculator tool [https://www.esrl.noaa.gov/gmd/grad/solcalc/]).
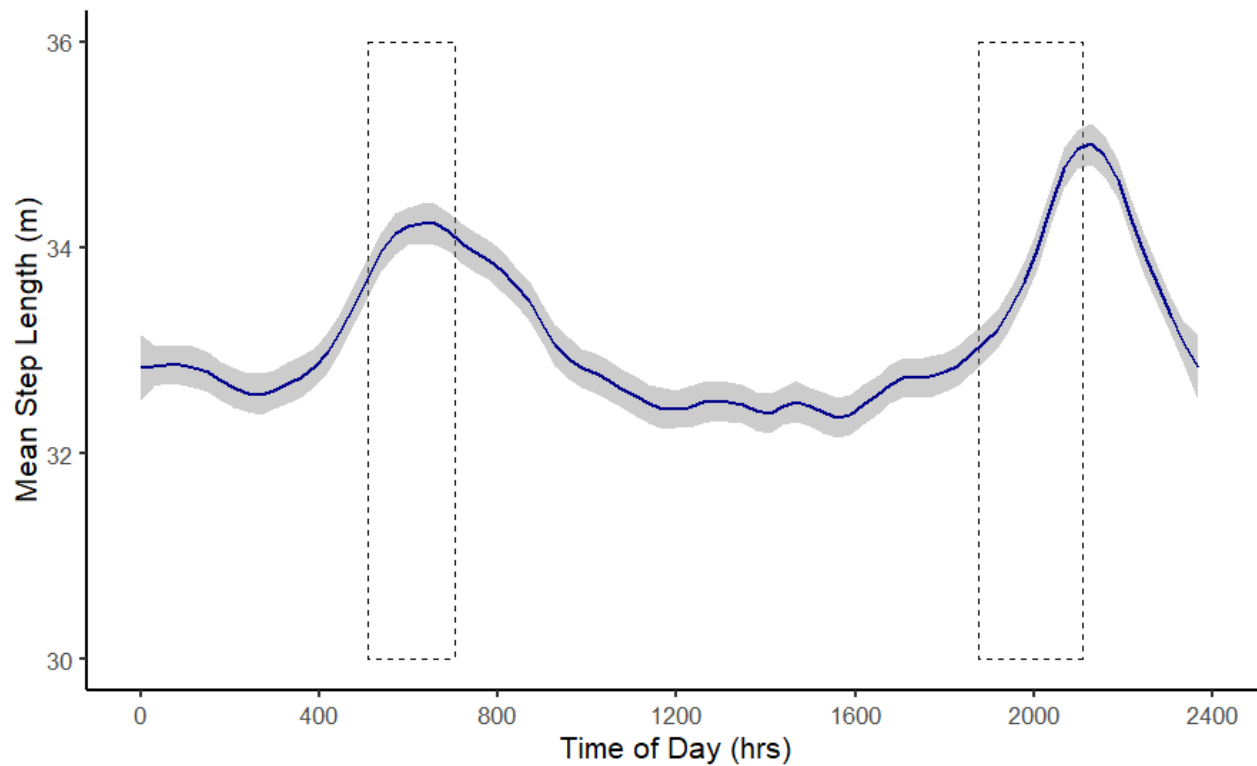
Fig A2. Interaction plots showing relationships for significant interactions between temperature and relative selection strengths (RSS) of variables of interest (A: Step length and temperature, B: Shade and temperature, C: Distance to bog and temperature, D: Distance to mixed forest and temperature) at progressively longer intervals between GPS locations (1: 20-minute, 2: 1-hour, 3: 2-hour, and 4: 4-hour). Patterns in the selection strength of interactions progressively weaken as the interval between GPS locations increases, in part explaining why other studies have not found consistent effects of temperature on moose movement.