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

2 # sensitive ungulate

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17

Abstract

Context

Warmer weather caused by climate change poses increasingly serious 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 modify behavior to avoid the negative consequences of acute heat will be crucial for understanding how animals will respond to warmer temperatures in the future.

Objectives

We studied the extent to which moose (*Alces alces*), a species known to be sensitive to heat, mitigates heat on hot summer days via multiple different behaviors: (1) reduced movement, (2) increased visitation to shade, (3) increased visitation to water, or (4) a combination of these behaviors.

Methods

We used GPS telemetry and a step-selection function to analyze movement and habitat selection by moose in northeastern Minnesota, USA.

Results

Moose reduced movement, used areas of the landscape with more 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.

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41 **Conclusions**

42 Research characterizing the behaviors animals use to facilitate thermoregulation will aid

43 conservation of heat-sensitive species in a warming world. The modeling framework presented

44 in this study is a promising method for evaluating the influence of temperature on movement and

45 habitat selection.

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47 **Key words**

48 climate change, habitat selection, habitat use, lidar, moose (*Alces alces*), resource selection, step-

49 selection function, thermal refugia

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Introduction

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53   Physiological performance peaks within a limited range of body temperatures in which

54 molecular, cellular, and systemic processes operate optimally. Body temperatures outside this

55 range impose functional constraints on these processes, including reductions in growth,

56 reproduction, activity, and immune function (Pörtner and Farrell 2008). Nevertheless, animals

57 routinely operate in environmental conditions that trigger suboptimal body temperatures (Boyles

58 et al. 2011; Sunday et al. 2014). This conundrum underlies two long-standing questions in

59 biological research: (1) How do animals mitigate suboptimal thermal conditions, and (2) how

60 effective are those efforts at mitigation? Rapid and ongoing responses to global climate change

61 by a multitude of animal species (Walther et al. 2002; Parmesan 2006; Hoegh-Guldberg and

62 Bruno 2010) increase the urgency of answering these questions.

63   Animals can relax the constraints of limited ranges of thermal tolerance by modifying

64 their behavior to reduce heat gain and dissipate heat at high temperatures. Such behavioral

65 thermoregulation has a long history of study in biological research (Cowles and Bogert 1944),

66 but this idea still offers fresh insight today. Animals can restrict movement to produce less

67 metabolic heat (Stelzner 1988; Broders et al. 2012), alter posture to reduce heat gain from

68 insolation or increase surface area to shed heat (Luskick et al. 1978; Bartholomew and Dawson

69 1979), pant to lose heat via evaporation (Campos and Fedigan 2009; McCann et al. 2013), or

70 visit thermal refugia (spaces that provide refuge from thermal stress caused by extreme

71 temperatures [e.g., burrows, wallows, shade cover]; van Beest et al. 2012; Hovick et al. 2014;

72 Kurylyk et al. 2015), among other behaviors. Identifying exactly which of these strategies

73 animals use to behaviorally thermoregulate, how much these strategies buffer against adverse

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

75 understanding their ability to increase ranges of thermal tolerance, which in turn increases our

76 understanding of how animals may adapt (or not) to increasing temperatures in a warmer future.

77   Recent advances in statistical modeling techniques provide opportunity to study

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

79 extension of the resource selection function modeling framework that explicitly incorporates

80 spatial and temporal animal movement characteristics to enable examination of fine-scale habitat

81 selection and movement behavior at biologically realistic scales (Forester et al. 2009; Thurfjell et

82 al. 2014; Duchesne et al. 2015). SSFs have primarily been used to model habitat selection

83 (Thurfjell et al. 2014), but recent theoretical development has demonstrated that they can also be

84 used to explicitly model movement behavior that changes in both space and time in relation to

85 landscape features (Avgar et al. 2016; Prokopenko et al. 2017; Ladle et al. 2019). By including

86 interaction terms between temperature, habitat covariates, and movement rates within SSFs, the

87 relative importance of temperature-dependent animal behaviors—including both resource

88 selection and movement rates—can be quantified in a single model.

89   We used the SSF modeling framework to examine behavioral thermoregulation in moose

90 (*Alces alces*), a species known to be sensitive to heat. Moose have undergone substantial

91 population declines across much of their southern range due in part to climate change (Lenarz et

92 al. 2009; Rempel 2011; Monteith et al. 2015). Moose experience heat stress starting at

93 temperatures as low as 14˚C (Renecker and Hudson 1986) or 17˚C (McCann et al. 2013) during

94 the summer. Moose prevent heat stress on hot days by using water, shade, and decreased activity

95 to shed heat via conduction and reduced exposure to radiation from the sun (Belovsky 1981;

96 Dussault et al. 2004; Broders et al. 2012; Street et al. 2015; McCann et al. 2016). At coarse

97 spatial and temporal scales, moose select for thermal cover (e.g., dense canopy in conifer forests)

98   during periods of high temperatures (Schwab and Pitt 1991; Demarchi and Bunnell 1995; van

99   Beest et al. 2012; Melin et al. 2014; Street et al. 2016; but see Lowe et al. 2010). However,

100   earlier studies have not established the relative importance of multiple different heat amelioration

101   strategies (e.g., seeking shade vs. reducing movement vs. visiting water) or identified thresholds

102   at which behavioral thermoregulation alters habitat selection.

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

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

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

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

107   enabled us to quantify the importance of several ways moose may alter behavior to

108   thermoregulate when it is hot: moose (1) decrease movement rates to decrease metabolic heat

109   production, (2) increase use of shade to decrease heat gain from solar radiation, (3) increase use

110   of water to increase heat loss via conduction, convection, and evaporation, or (4) use some

111   combination of each of these.

112

113   **Materials and Methods**

114   **Study area**

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

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

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

118   forests in the south to Canadian boreal forests in the north (Pastor and Mladenoff 1992). Upland

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

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

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

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

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

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

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

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

127   Natural Resources).

128

129   **Animal Capture and GPS Telemetry**

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

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

132   (4.0 mg ml^{-1}) carfentanil citrate and 1.2 ml (100 mg ml^{-1}) xylazine HCl, and we used 7.2 ml (50

133   mg ml^{-1}) naltrexone HCl and 3 ml (5 mg ml^{-1}) yohimbine HCl as antagonists (Roffe et al. 2001;

134   Lenarz et al. 2009). We fitted immobilized moose with global positioning system (GPS) collars

135   (Lotek Wireless, Inc., Newmarket, Ontario, Canada). Animal capture and handling protocols met

136   American Society of Mammalogists recommended guidelines (Sikes and Animal Care and Use

137   Committee of the American Society of Mammalogists 2011) and were approved by the

138   University of Minnesota Animal Care and Use Committee (Protocol Number: 1309-30915A).

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

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

141   with dilution of precision values ≤ 5 (Lewis et al. 2007) and removed locations that were not

142   biologically possible (i.e., removing locations where the distance between locations would have

143   exceeded the distance a moose could have moved in a 20-minute period, assuming a maximum

144   speed of 30-km/hour). Data used in this analysis include only locations between May 1 and

145   September 31—dates that coincide with average daily maximum temperatures above the

146   threshold believed to induce heat stress for moose (Renecker and Hudson 1986). Location and

147   activity data within 2 weeks of death or collar failure were censored from our data, and only full

148   months of data were used in analysis. Our analysis included 153 moose-months from 24 moose.

149   Moose were adults at capture except for one moose that was a yearling (1.8 years old), and 17 of

150   24 moose were females.

151

152   **Model Covariates**

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

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

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

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

157   vegetation structure (Vierling et al. 2008; Davies and Asner 2014). Lidar data were collected

158   over our entire study area during leaf-off conditions in May 2011 as part of the Minnesota

159   Elevation Mapping project (Minnesota Geospatial Information Office). Lidar data were collected

160   from a fixed wing airplane at an altitude of 2,000-2,300 m above ground level using discrete-

161   return laser scanning systems (ALS60, ALS70, or Optech GEMINI). Side overlap was 25% with

162   a scan angle of $\pm$ 20°. Nominal point spacing and pulse density varied due to incomplete overlap

163   of adjacent flight-lines. Average nominal pulse density was 1 pulse/m^2. We calculated height of

164   discrete returns above ground by subtracting ground elevation based on a lidar-derived Digital

165   Elevation Model from the return elevation. Lidar data met the National Standard for Spatial

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166   Database Accuracy and had a vertical accuracy RMSE of 5.0 cm and a horizontal accuracy of

167   1.16 m.

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

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

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

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

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

173   refer to lidar-derived canopy vegetation density as "shade".

174   Vegetation cover types were determined using the 2011 National Land Cover Database

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

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

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

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

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

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

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

182   amount of shade and proportion of conifers increases. Selection of cover types may be dependent

183   on proximity to other cover types, and GPS error may lead to underestimation of selection of

184   cover types covering small areas (Conner et al. 2003; Martin et al. 2018). We therefore

185   calculated the Euclidean distance of each pixel in our study area from each of our chosen

186   vegetation cover types using ArcMap 10.4 (Esri, Redlands, California, USA). Euclidean

187   distances were 0 when an animal was within the land cover type of interest.

188   Temperature data were obtained from two weather stations within our study area (KBFW

189   in Silver Bay and KCKC in Grand Marais; MesoWest; Fig. A1). These stations are operated by

190   the National Oceanic and Atmospheric Administration according to national standards and report

191   temperatures at 20-minute intervals. Moose locations were individually matched with the nearest

192   weather station (by distance) and nearest temperature recording (by time). Moose locations were

193   on average 33 km from the nearest weather station and 7 minutes from the closest recorded

194   weather observation in time.

195

196   **Statistical Analysis**

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

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

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

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

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

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

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

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

205   interaction with another variable of interest (Avgar et al. 2016; Prokopenko et al. 2017; Ladle et

206   al. 2019). Interaction coefficients detail how temperature influences step length and selection of

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

208   course of each 24-hour period (Fig. A2), we adjusted step lengths prior to inclusion in the model

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

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

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

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

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

214

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

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

217   Temp*StepLength,

218

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

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

221   pseudoreplication (Fortin et al. 2005; Craiu et al. 2008; Duchesne et al. 2010), and checked to

222   ensure that VIFs between main effects were adequately low (O'Brien 2007; Dormann et al.

223   2013). We then conducted k-fold (k=5) cross-validation on our final model and calculated

224   Spearman rank correlation (mean of 50 replications) to evaluate model fit (based on the methods

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

226   minimum interval between GPS locations required to detect biologically significant interactions.

227   All analyses were conducted using R statistical software (R Core Team 2018).

228

229   **Results**

230   **Moose Movement and Resource Selection**

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

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

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

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

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

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

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

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

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

240   areas near marsh or open water. Habitat use by moose was consistent throughout our study

241   period (i.e., month-to-month changes in distance to vegetation cover types were small; Fig. A3).

242   Moose decreased movement rates at hotter temperatures (Fig. 2A). The mean step length

243   at all temperatures above 20°C was below the overall mean step length controlling for time of

244   day. At each standardized step length > 0 m (i.e., steps that were longer than average for a given

245   time of day), the odds of moose taking a step of that length was higher at 0°C than at 15°C, and

246   higher at 15°C than at 30°C. At 0°C, the odds that moose would move 100 m more than average

247   in 20 minutes were substantially higher (RSS = 1.074; 95% CI = 1.025-1.126) than at 15°C (RSS

248   = 0.849; 95% CI = 0.777-0.928), which were in turn substantially higher than at 30°C (RSS =

249   0.672; 95% CI = 0.590-0.765).

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

251   strength increased with increasing vegetative cover at 30°C, while it decreased with increasing

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

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

254   75% vegetative cover were substantially lower (RSS = 0.265; 95% CI = 0.239-0.295) than at

255   15°C (RSS = 0.640; 95% CI = 0.523-0.782), which were in turn substantially lower than at 30°C

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

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

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

259   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

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

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

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

263   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

264   30˚C (RSS = 0.594; 95% CI = 0.353-0.998 at 500 m), though odds did not significantly differ

265   between 15˚C and 30˚C.

266

267   **Model validation**

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

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

270   0.47 for observed steps.

271

272   **Effects of temporal scale on interactions**

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

274   locations occur at longer intervals. When 20-min interval GPS data are rarified to 1-hr, 2-hr, and

275   4-hr intervals and used to fit the same SSF, interactions become progressively less biologically

276   meaningful (Fig. A4). As the intervals increase, differences across temperatures for step length,

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

278   mixed forest shrink, but more gradually.

279

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Discussion

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281   In this paper, we developed a modeling framework to test multiple competing (but not

282   mutually exclusive) hypotheses on behavioral responses by animals to heat. We used this

283   framework to model behavioral responses by moose, an ungulate known to be sensitive to heat.

284   Moose altered both movement and habitat selection to behaviorally thermoregulate during hot

285   periods. Moose reduced movement and moved nearer to or stayed within shade, bogs, and mixed

286   forest at high heat, even while avoiding shade and bogs at cooler temperatures (Fig. 2). This

287   pattern links previous findings of separate studies. First, moose prefer to forage in areas with low

288   canopy cover because canopy cover is generally inversely related to forage availability (Lone et

289   al. 2014). Second, moose prefer to use bed sites under dense forest canopy in wet lowland forests

290   during the day (McCann et al. 2016), where moose have access to less forage but more

291   protection against heat gain from solar radiation and more capacity to lose heat to wet ground via

292   conduction. Moose therefore face a steep tradeoff during periods of heat—areas that are good for

293   foraging may not be good for avoiding heat. Selection for shade and shorter step lengths as

294   temperatures increase indicates that moose forego foraging in favor of bedding down under

295   shade as temperatures increase. Earlier studies have documented moose shifting activity to

296   cooler evenings and nights on hot days (Dussault et al. 2004; Montgomery et al. 2019), which is

297   consistent with this trade-off.

298   The vegetation cover types used more by moose during warm weather further indicate

299   that moose face a tradeoff between foraging and thermoregulation during periods of heat. In

300   general, moose are more likely to find greater quantities of forage in cover types that do not

301   provide thermal cover, while cover types that provide thermal cover are less likely to provide

302   forage. For example, upland mixed forest has some available forage, but forage availability is

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303 highest in this cover type in young forests with little canopy cover. Similarly, bogs in Minnesota

304 are largely populated by black spruce, tamarack, and alder, all of which can provide thermal

305 cover but are unpalatable for moose. Birch (*Betula* spp.) and willow (*Salix* spp.) are more

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

307 compensate for unpalatable species dominating the canopy layer.

308   Further studies would be helpful for demonstrating how common trade-offs between

309 thermoregulation and foraging are among ungulates. Reductions in activity during periods of

310 heat are widespread among ungulates, having been documented in a diverse array of ungulates

311 that include moose, mule deer (*Odocoileus hemionus*; Sargeant et al. 1994), bighorn sheep (*Ovis*

312 *canadensis*; Alderman et al. 1989), Alpine ibex (*Capra ibex*; Aublet et al. 2009; Mason et al.

313 2017), Alpine chamois (*Rupicapra rupicapra*; Mason et al. 2014), common eland (*Taurotragus*

314 *oryx*; Shrestha et al. 2014), black wildebeest (*Connochaetes gnou*; Vrahimis and Kok 1993), blue

315 wildebeest (*Connochaetes taurinus*; Shrestha et al. 2014), impala (*Aepycerus melampus*;

316 Shrestha et al. 2014), and greater kudu (*Tragelaphus strepsiceros*; Owen-Smith 1998).

317 Nevertheless, the relative importance of reducing activity is not often compared directly to other

318 strategies used by ungulates to reduce heat stress, and reductions in activity may not always

319 result in reduced foraging opportunity, which depends on landscape structure (i.e., distance

320 between foraging sites and bed sites with adequate thermal cover).

321   Studies on the contexts in which tradeoffs between foraging and thermoregulation

322 become particularly acute will also be important in a warming future. Environment and

323 nutritional condition may play a role in shaping such tradeoffs. For example, North American elk

324 (*Cervus canadensis*) prioritize reducing thermoregulatory costs over forage quality in low-

325 elevation desert populations but not in high-elevation mountain populations, and individuals with

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326   low fat reserves prioritize reducing thermoregulatory costs over forage quality most strongly

327   (Long et al. 2014). Body size may also play a role in modulating tradeoffs between foraging and

328   thermoregulation. Adult male Alpine ibex, which are substantially larger than females, reduce

329   time spent foraging more than females when it is hot (Aublet et al. 2009). Common eland and

330   blue wildebeest reduce afternoon activity all year round, but smaller impala reduce afternoon

331   activity only during the summer (Shrestha et al. 2014). The effects of environmental variation,

332   nutritional condition, or body size on thermoregulatory behavior could be answered in larger data

333   sets using our modeling framework by building SSFs for each individual and testing for

334   statistical effects of a variable of interest (e.g., fat reserves, body size) on the RSS of a variable

335   of interest (e.g., step length at a given high temperature).

336   Determining the relative importance of features on the landscape for mitigating heat

337   stress will also be important in a warming future. In our study, moose used shade far more than

338   water to ameliorate heat during hot weather. Moose are commonly observed in bodies of water,

339   and anecdotal evidence suggests that moose use water to shed heat (Schwab and Pitt 1991;

340   Demarchi and Bunnell 1995). Our analysis, however, indicates that moose do not often use open

341   water and marsh to mitigate heat stress; they prefer to seek shadier vegetation cover types.

342   Nevertheless, they do increase use of woody bogs—where both shade and some water are

343   usually available—as temperatures increase. This is consistent with a previous study (McCann et

344   al. 2016) that found that moose prefer bed sites with both canopy cover and relatively high soil

345   moisture. Other ungulates may use different features of the landscape to mitigate heat stress. For

346   example, mountain goats (*Oreamnos americanus*) move nearer to persistent snow cover during

347   hot weather, but do not seek shade (Sarmento et al. 2019). Step-selection functions that include

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348   interactions with temperature offer a simple way to test for the relative importance of a wide

349   variety of different landscape features for thermoregulation.

350   Frequent GPS locations enabled us to detect responses to heat by moose and may explain

351   why previous attempts to characterize moose movement patterns failed to reveal a strong

352   relationship between temperature and movement rates (Dussault et al. 2004; Montgomery et al.

353   2019). Moose spend about half of their day foraging during the summer, with foraging bouts

354   interspersed by periods of rumination at bed sites. Periods of rest and rumination are typically

355   distinct and occur at regular intervals of roughly 2 hours (Renecker and Hudson 1989; Moen et

356   al. 1996). As the interval between GPS locations increases, the chance that both ambulatory

357   foraging bouts and stationary ruminating bouts are aggregated into a single GPS fix increases,

358   which homogenizes step lengths (Moen et al. 1996). Frequent GPS locations reduce the

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

360   intervals, effect sizes of interactions between temperature and movement rates are progressively

361   reduced (Fig. A4). Because many species have idiosyncratic movement behaviors, movement

362   studies may require intervals between GPS locations within a specific range to answer research

363   questions concerning animal movement. This is an important consideration for researchers

364   planning studies of animal movement. Researchers should carefully consider the frequency of

365   GPS locations before deploying GPS collars and recognize that GPS data that is too sparse may

366   not be suitable for studies of some movement behaviors.

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

368   Many moose populations at the southern edge of their distribution (including our study area)

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

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

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

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

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

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

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

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

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

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

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

380 forest.

381   Some measure of fitness (or a proxy for fitness) would make it possible to directly link

382 behavioral strategies to a population-level response to large-scale drivers like climate change.

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

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

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

386 need to behaviorally thermoregulate. Although we did not link behavior to fitness in this study,

387 identifying and quantifying patterns of behavior allows researchers to explicitly test for effects

388 on fitness in subsequent studies. For example, development of conceptual and modeling

389 frameworks to identify and quantify "green wave surfing" behavior (by which animals migrate

390 along paths of rapidly greening forage) in migratory ungulates (Bischof et al. 2012; Merkle et al.

391 2016; Aikens et al. 2017) allowed researchers to later quantify a connection between green wave

392 surfing and fitness (Middleton et al. 2018). Our study could be used as a foundation for further

393 analyses along these lines, or to parameterize mechanistic models of moose energetic balances

18

394   under various climate scenarios, land management strategies, or disturbance regimes to project

395   the outcomes of conservation actions taken to benefit moose.

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

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

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

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

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

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

402   inference on how animals change movement and habitat selection in space and time in response

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

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

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

406   SSFs that incorporate interactions between temperature and other variables of interest can

407   characterize changes in movement behavior and habitat use in response to differences in

408   temperature.

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

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

411   vegetation cover types that they avoided at cooler temperatures. Moose did not regularly use

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

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

414   Behavior changed at thresholds near (though somewhat above) previously documented heat

415   stress thresholds (Renecker and Hudson 1986; McCann et al. 2013): step lengths decreased at

416   temperatures above 20˚C, and selection patterns for shade reversed above 15˚C. Future research

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417   characterizing strategies for behavioral thermoregulation and consequences of those strategies

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

419   species.

420

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429

Author Contributions

431   JA and RM conceived and designed the study; RM collected the data; JA, MJ, and JM analyzed

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

433   drafts and gave final approval for publication.

434

Data Availability

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

437

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643

Figures

Fig. 1 The physical characteristics of the surrounding environment greatly influence the thermal landscape for animals. Fig. 1A represents an environment (conifer forest) where heat gain may be decreased by reducing exposure to radiation, Fig. 1B represents an environment (marsh) where heat loss may be increased by conduction, and Fig. 1C represents an environment (clear cut) that offers neither relief from radiation nor opportunities to disperse heat via conduction. Moose likely face tradeoffs between forage availability and thermal relief.
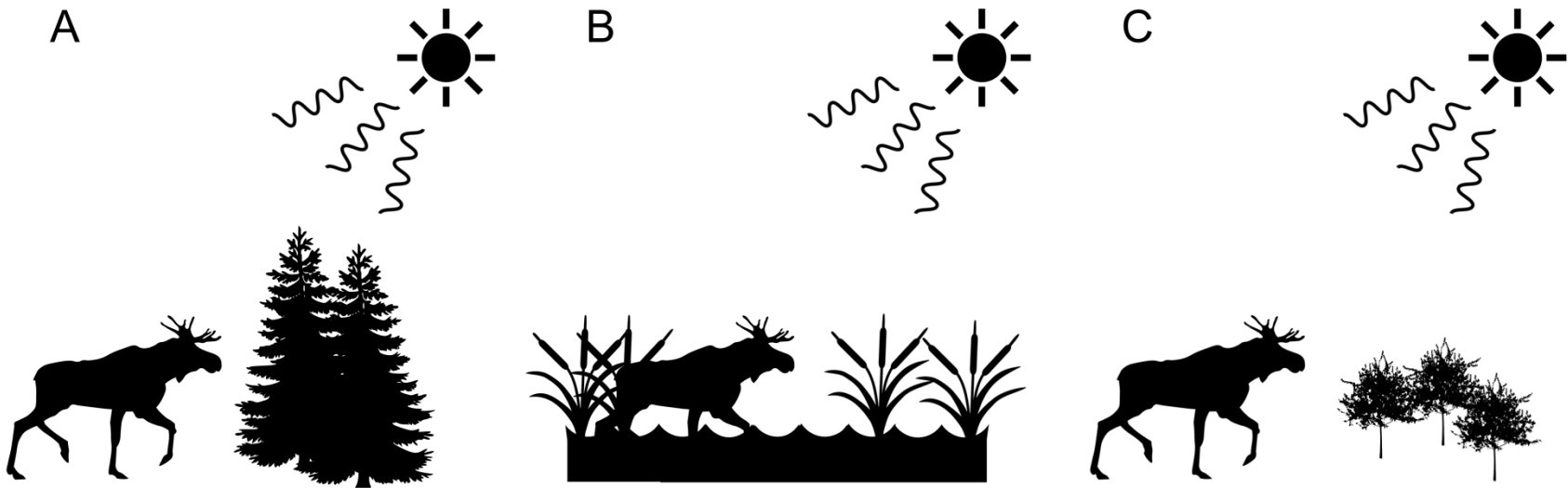
652   **Fig. 2** Interaction plots showing relationships for significant interactions between temperature and relative selection strengths (RSS) of

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

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

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

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

657   at 30˚C).

658
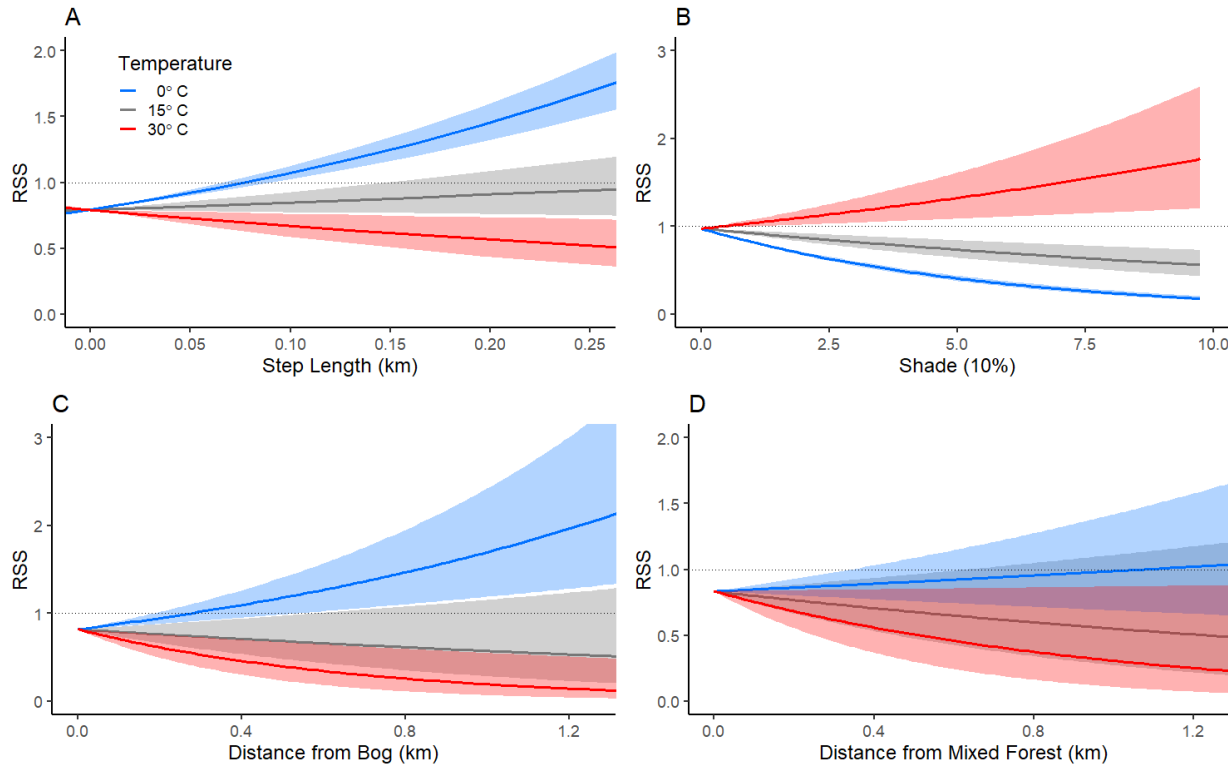
Tables

Table 1 Variables incorporated in the step-selection function of moose movement and habitat selection and justification for inclusion 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 Comparison of temperatures at the two weather stations used in this study (KCKC in Grand Marais and KBFW in Silver Bay). The red line indicates a 1:1 relationship. Temperatures at KCKC followed the regression line 1.74 + 0.821*KBFW, where "KBFW" indicates the temperature at the KBFW station. R^2 = 0.881 for the regression equation. Temperatures were thus slightly warmer at KCKC at very low temperatures (less than ~2˚C), but usually slightly cooler (e.g., when it was 30˚C at KBFW, the expected temperature at KCKC was 26.4˚C). Variation in temperature on the landscape was thus much smaller than temperature across the day or summer.
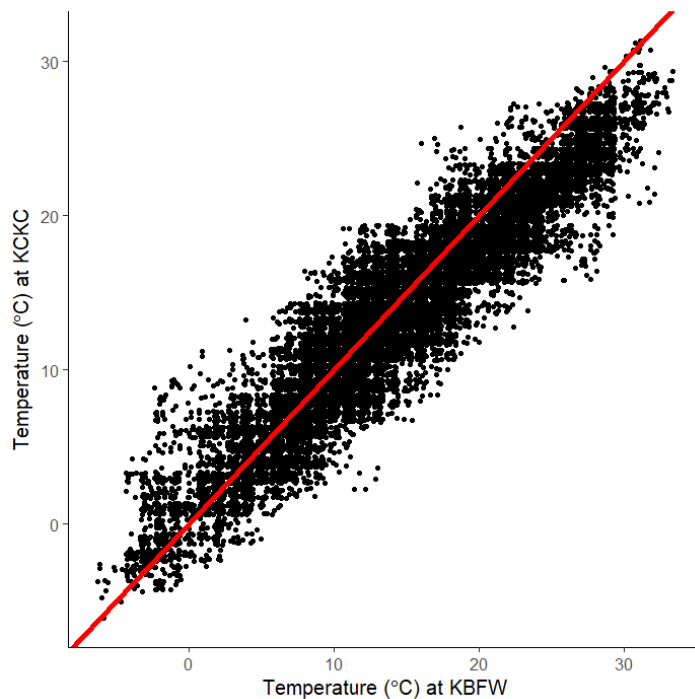
Fig. A2 Lowess regression of mean step length across times of day (20 min. increments). The gray ribbon represents the 95% confidence interval for the regression line. Moose movement rates varied slightly but consistently over the course of the day, with movement rates peaking during crepuscular periods. 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/]).
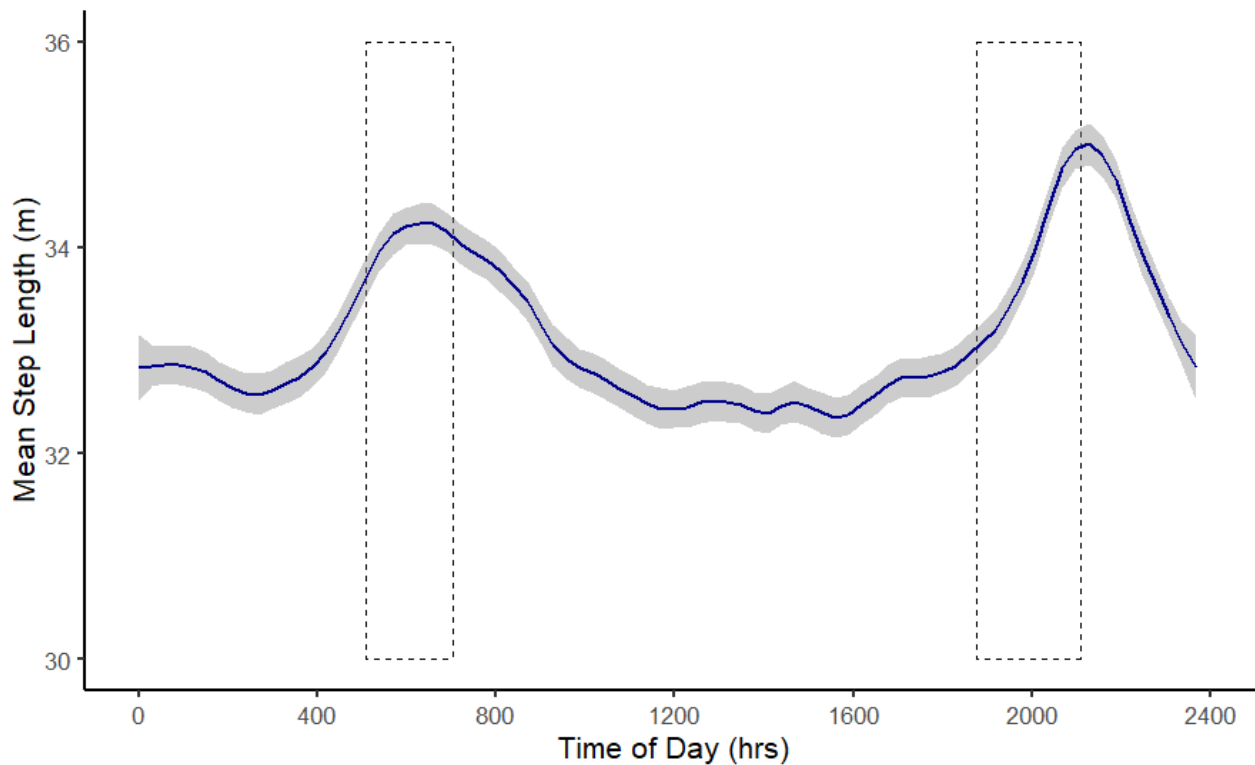
Fig. A3 Boxplots showing monthly changes in distance to cover types of interest (A: Distance to bog, B: Distance to marsh, C: Distance to water, D: Distance to conifer forest, E: Distance to mixed forest). Month-to-month differences in habitat use are small, indicating that patterns observed from our SSF reflect habitat selection throughout our study period and are not influenced by one-time phenological events occurring during our study period (e.g., parturition movements by females during May, or the emergence of aquatic plants during June).
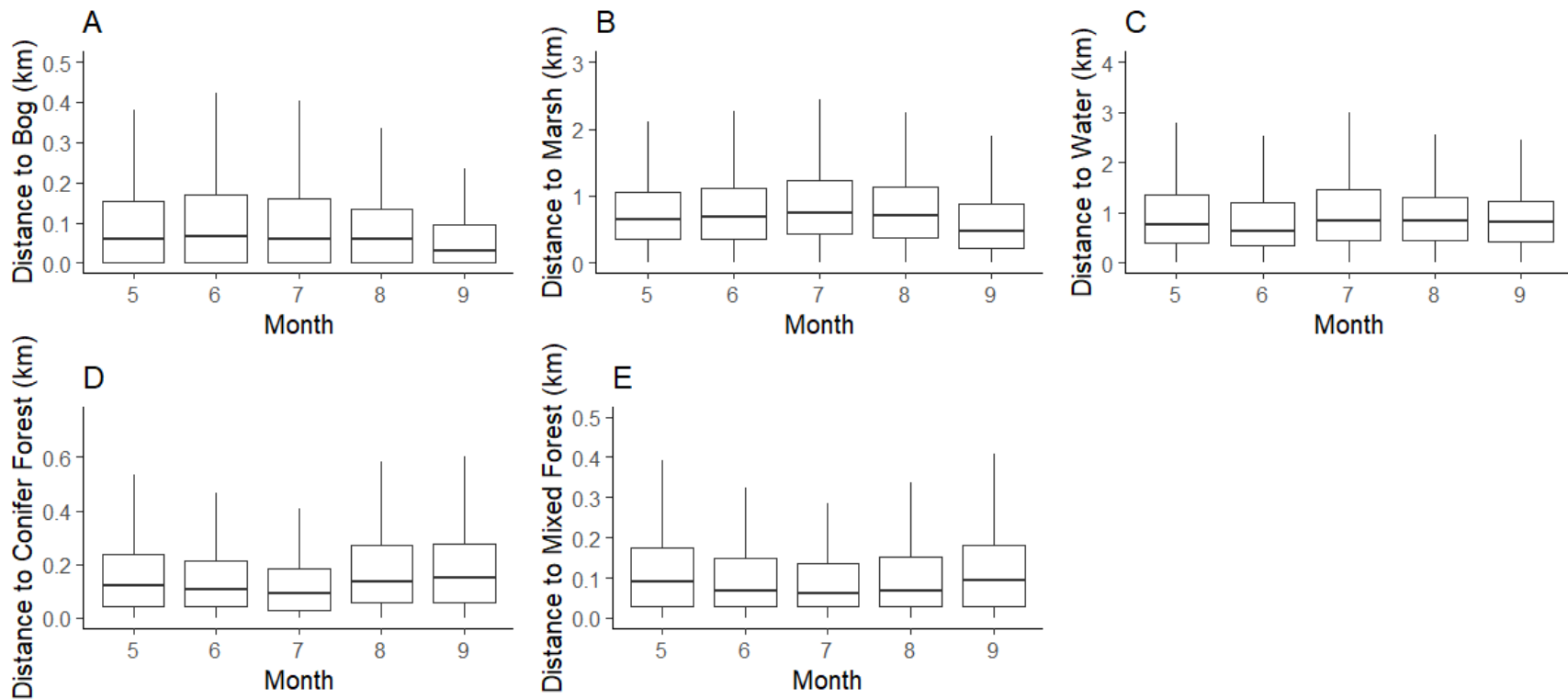
Fig. A4 Interaction plots showing relationships for significant interactions between temperature and relative selection strengths (RSS) of variables of interest (A: Step length and temperature, B: Shade and temperature, C: Distance to bog and temperature, D: Distance to mixed forest and temperature) 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.