1 Mammalian body size is determined by interactions between climate, urbanization, and life
2 history traits
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47 **Abstract:** Anthropogenically-driven climate warming is a hypothesized driver of animal body

48 size reductions. Less understood are effects of other human-caused disturbances on body size,

49 such as urbanization. We compiled 140,499 body size records of over 100 North American

50 mammals to test how climate and urbanization, and their interactions with species traits, impact

51 body size. We tested three hypotheses of body size change across urbanization gradients; urban

52 heat island effects, fragmentation, and resource availability. Our results unexpectedly

53 demonstrate urbanization is more tightly linked with body size changes than temperature, most

54 often leading to larger individuals, thus supporting the resource availability hypothesis. In

55 addition, life history traits, such as thermal buffering, activity time, and average body size play

56 critical roles in mediating the effects of both climate and urbanization on intraspecific body size

57 trends. This work highlights the value of using digitized, natural history data to track how human

58 disturbance drives morphological change.

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70 **INTRODUCTION**

71 Body size is an easily measured, integrator trait that scales with many other life-history

72 characteristics of organisms (Gould 1966; Brown & Maurer 1986; Brown et al. 1993). Because

73 of this, understanding drivers of body size has been a central goal of ecology over the last half

74 century. Macroscale studies of body size across broad environmental gradients date back

75 centuries, to the seminal work of Carl Bergmann (1847), although with much debate about the

76 generality of patterns and underlying mechanisms (Ashton et al. 2000; Meiri & Dayan 2003;

77 Riemer et al. 2018). Some species - but not all - follow predicted responses to temperature, with

78 smaller average body size in warmer climates. In addition to temperature, food availability

79 strongly determines species' body size changes (Alroy 2001; Pineda-Munoz et al. 2016).

80   Much less attention has been paid to anthropogenic influences on body size that play out

81 at the local or regional scale, which provides a distinct set of challenges and opportunities for

82 organisms. While urbanization may increase potential for novel human-caused conflict

83 (including traffic) and predation, these novel environments can also lead to decreased predation

84 rate (Fischer et al. 2012) and increased food resources. The complexity of urban environments

85 provides an opportunity to examine species responses to a variety of major ecological gradients

86 in real time, and to test the applicability of longstanding ecogeographic rules within the human-

87 built environment. For example, Ives et al. (2016) found Australian cities harbor a large number

88 of threatened species, which may be due to a high amount of landscape heterogeneity (e.g. plant

89 cultivation) in urban areas.

90   Understanding the magnitude and direction of body size variation due to human

91 alteration of landscapes is complicated by multiple possible, non-mutually exclusive drivers.

92 First, due to human activity and built infrastructure, cities are generally warmer than surrounding

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93   areas, a phenomenon known as the urban heat island effect (Oke 1982). Animals inhabiting

94   warmer urban heat islands are predicted to be smaller in body size based on the general tendency

95   for species to decrease in size with increasing temperature (Blackburn & Hawkins 2004; Gardner

96   et al. 2011; Rapacciuolo et al. 2017; Weeks et al. 2019). There has been limited empirical support

97   for urban heat island effects driving decreases in body size (but see Merckx et al. 2018 for

98   insects), especially for endotherms (Pergams & Lacy 2008). However, little attention has been

99   paid to which body size metrics are used to make claims about heat island impacts. In a recent,

100   large-scale study of body size variation in the North American deer mouse (*Peromyscus*

101   *maniculatus*), Guralnick et al. (2020) examined both body mass and head-body length and found

102   mice were shorter (but not lighter) in more urbanized areas. Those authors postulated a heat

103   island effect could be driving body length changes separate from mass changes, but also

104   suggested this could represent a selective response to avoid detection (i.e., crypsis). Second,

105   heterogeneity in urban areas can contribute to increased food resources and water availability

106   compared to rural areas (McKinney 2008), which could further mediate body length or mass

107   change in urban areas (i.e., a resource rule, McNab 2010). It is also possible that the

108   compounding effect of urbanization on top of climate change may amplify adaptive or plastic

109   changes in body size. Finally, Schmidt and Jensen (2003, 2005) suggested that species that

110   experience landscape fragmentation driven by urbanization and an increased human footprint

111   should either go extinct or adapt through changes in life history traits, namely increasing body

112   size for smaller species and decreases for larger species. Each of these hypotheses have clear,

113   alternate predictions about the overall effects of urbanization, and can be emplaced in the

114   broader context of overall climatic gradients.

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115   Mammals represent a good test case for examining the potentially multifaceted effects of

116   climate and urbanization on body size in the same modeling framework, in order to understand

117   the relative importance of different drivers across species with widely varying body sizes and life

118   history traits. Mammals have evolved to fill a large variety of niches including aquatic,

119   terrestrial, and even subterranean habitats, often facilitated by the evolution of key functional,

120   morphological, or behavioral traits. These traits are expected to strongly mediate current and

121   future responses of organisms to climate change. Few studies have directly examined how these

122   factors may influence spatiotemporal trends to recent global change responses of mammals (but

123   see Lindstedt & Boyce 1985; McCain & King 2014; Naya et al. 2017). Habitat buffering, a suite

124   of behaviors such as nocturnality, or spending portions of the life cycle underground, may be

125   critical for coping with unsuitable climatic conditions especially in the short term; body size

126   changes may thus be weaker in species with such buffering capability (Johnson 1931; Terrien et

127   al. 2011). Finally, mammals are well-sampled in many biodiversity datasets, with body size

128   measurements often taken in the field as part of long-standing collection practices. This creates

129   an opportunity to analyze records for a vertebrate clade spanning over 100 years, providing

130   ample data, albeit with associated challenges of dealing with spatiotemporal collecting biases

131   which need to be carefully considered in downstream modeling.

132   In this study, we compiled multiple datasets containing 140,499 mass and body length

133   records spanning more than 100 mammal species and 80 years to address broad-scale spatial

134   trends of mammalian body size (Fig. 1, S1). Our overarching question is whether and how much

135   climate and human population density, the latter of which represents a proxy for the human built

136   environment, impact mammal body size. We first addressed the relationship between body mass

137   and head-body length, as each is commonly used as a body size metric but the former can vary

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138   seasonally due to age, reproductive status, or food availability (McNab 1980), potentially

139   weakening mass-length allometries at range-wide scales (Guralnick et al. 2020). We then use a

140   hierarchical modeling framework to identify the main drivers of body size variation, accounting

141   not only for climate and urbanization but also broad differences in habitat and species-specific

142   trends. Drawing on Bergmann's Rule, we predicted that temperature would negatively impact

143   both metrics of body size (i.e. increasing temperatures lead to smaller size). We also expected

144   that increasing human population density would drive smaller body size due to heat island

145   effects, thereby amplifying Bergmann's-like patterns. Alternatively, and given recent results

146   from single species studies (e.g., Guralnick et al. 2020), it may also be that body mass increases

147   while body length decreases in urban areas as increased anthropogenic food availability (e.g.,

148   garbage or human provisioning of food) allows for more weight (Robinette et al. 1973;

149   Beckmann & Berger 2003) but need for crypsis or heat island effects drive decreasing length.

150   Further, urbanized areas may mimic islands given often fragmented habitats, driving larger

151   species to decrease in size and smaller species to increase in size.

152   To develop a more integrative framework for understanding body size variation in

153   mammals, we extended our work beyond focusing on broad-scale climate and urbanization

154   gradients and examined life history traits that are related to species thermal biology, which are

155   likely to modify and interact with both these drivers, especially ability to buffer thermal

156   environments. Therefore, we predicted weaker responses of body size change from species that

157   hibernate or utilize habitat buffering as they are able to avoid extreme climates. We also

158   considered traits such as diurnality and expected that nocturnal mammals should increase in size

159   more than diurnal species in urban areas since they can more easily avoid humans but still

160   benefit from food resources. Lastly, based on the hypothesis of more fragmented, island-like

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161 habitats in human built environments, we predicted that larger species may decrease in body size

162 and smaller species increase in size in areas of higher human population density. Small size is

163 also predicted to be favored as a greater number of microhabitats are available to escape

164 unfavorable temperatures and avoid human detection (Cardillo et al. 2005; Huey et al. 2012;

165 Scheffers et al. 2014).

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167 **METHODS**

168 **Data sources & aggregation**

169 We obtained mammal body size data from three repositories: VertNet (Guralnick & Constable

170 2010), the National Ecological Observatory Network (NEON 2019;

171 https://www.neonscience.org/), and the North American Census of Small Mammals (NACSM;

172 Calhoun 1948, 1949, 1950, 1951, 1956; Calhoun & Arata 1957a, 1957b, 1957c, 1957d).

173 Standard body mass and total body length measures were extracted from the VertNet corpus

174 following the approach of Guralnick et al. (2016). NEON data were obtained using the

175 "neonUtilities" R package (Laney & Lunch 2019), but only body mass was used from NEON

176 survey events because accurate length measures are difficult to obtain on live, unanesthetized,

177 mammals (Guralnick et al. 2020). We found no systematic biases of body mass measures from

178 NEON or other sources. NACSM data were obtained via manual digitization from published

179 reports, and were extracted for a subset of species that had body size measurements and which

180 were also obtained from VertNet and NEON. We aggregated VertNet data with corresponding

181 species from NEON and NACSM and harmonized data field names across the three sources.

182 Any migratory species were removed as they can experience a wide breadth of environmental

183 conditions. Measures of head-body length were then derived by subtracting tail length from total

184 length for each individual. As a preliminary step, we filtered the data to those species with a

185 minimum of 100 records for body mass or length count.

186

187 **Data filtering**

188 Additional filtering included removal of records lacking; 1) latitude and longitude; 2) sex,

189 including ambiguous sex assignments (e.g. "female?"); 3) date information – we required month,

190 day, and year for each record. However, for some specimen records with missing locality, we

191 first aimed to manually georeference data when possible using the protocols of Chapman and

192 Wieczorek (2006), which uses a combination of Google Maps (https://www.google.com/maps)

193 and the MaNIS georeferencing calculator (Wieczorek et al. 2001; http://manisnet.org/gci2.html).

194 Manual curation based on locality was also necessary in some instances. For example, several

195 records of *Canis lupus* came from zoos or sanctuaries; all zoo records were removed by hand.

196 We next created two additional fields from the record dates, "season collected" and "decade".

197 Month of collection was used to bin the records into spring (March-May), summer (June-

198 August), fall (September-November), and winter (December-February) seasons. In some species,

199 tail length is not reported due to very small or missing tails, and in those cases we relied on total

200 length. We also filtered juveniles from the dataset based on age assignments in the Darwin Core

201 field "lifeStage" (for VertNet) or based on body size measurements below a lower threshold for

202 each individual species based on literature searches and reputable online databases (see Table

203 S1). To remove any additional erroneous data values (e.g., digitization errors), we used a 95%

204 dispersion-based threshold using the "OutlierDetection" R package (Tiwari & Kashikar 2019).

205 Taxonomy was updated for all records to ensure scientific names were synonymous across data

206 sources.

207

Relationship between body mass and head-body length

209 We ran simple univariate linear regressions where $\log_{10}$ head-body length predicts $\log_{10}$ body

210 mass for each species. Correlations were generally weak among species as indicated by the vast

211 majority of the fits with $r^2 < .5$ (Table S1). As such, we compiled two body size datasets: body

212 mass and head-body length which were used separately as response variables in downstream

213 models.

214

Population density and climate

216 As a proxy for urbanization, we used high-resolution (1 x 1 km) decadal human population

217 density data for the conterminous USA (years 1940-2010) from Fang and Jawitz (2018). We

218 selected human population density over impervious land cover or Human Footprint Index

219 (Venter et al. 2016) as our measure of urbanization because it more directly accounts for

220 anthropogenic effects (e.g. food waste) and encompasses the range of mammalian species

221 collection dates used in this study. Human population density data were appended to each record

222 by first aggregating density data to a resolution of 10 x 10 km and indexing this value by decade

223 collected and record locality using an R (R Core Team 2018) script. Human population density

224 was $\log_{10}$ transformed for statistical analyses. Historical climate data were obtained from the

225 PRISM Climate Group (PRISM Climate Group, 2020) at 4 km resolution for both historical and

226 contemporary body size observations. We extracted mean annual temperature (MAT) and mean

227 annual precipitation (MAP) from PRISM based on observation year and geocoordinates.

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Spatial regions

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230 To control for habitat differences across our region of interest, we included ecoregional

231 membership as a random effect in each model. We used the United States Environmental

232 Protection Agency (EPA) Level 1 ecoregions (https://www.epa.gov/eco-research/ecoregions),

233 but further divided three ecoregions given the large climate and latitudinal range. We split the

234 'Great Plains', 'Northwestern Forested Mountains', and 'North American Deserts' ecoregions at

235 42 degrees latitude and renamed the ecoregions: 'Northern and Southern Great Plains', 'Northern

236 and Southern Cordilleras', and 'Northern and Southern Desserts', respectively (Fig. 1).

237

238 **Phylogeny and mammal traits**

239 We obtained a global mammal phylogeny from Upham et al. (2019;

240 http://vertlife.org/data/mammals/) and pruned the tree to match the species present in the two

241 datasets (body mass, n = 101; head-body length, n = 99). We also compiled life history traits for

242 the final species sets that likely influence body size response to environmental change. These

243 traits include hibernation ability (binary, Y/N), habitat buffering (e.g. fossorial vs. terrestrial;

244 binary, Y/N), daily activity pattern (diurnal, nocturnal, or both), and average body size binned

245 into small (<500g; <200mm) and large (>500g; >200mm) categories (Fig. S2, sources provided

246 in Table S1). Sensitivity analyses of mean average body size binned into different sizes (e.g.

247 ranging 450-550g, 150-250mm) yielded the same model results.

248

249 **Mixed-modeling framework**

250 To examine drivers of mammalian body size variation, we initially used linear mixed-effects

251 models (LMM), using the R package *lme4* (Bates et al. 2014). We $\log_{10}$ transformed measures of

252 body mass and HB length as mammal body size ranges vary by orders of magnitude (Brown

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253 1995). In addition, we log$_{10}$ transformed human population density and log transformed MAP to

254 normalize data. We mean-centered and standardized all continuous predictors to have standard

255 deviations of 1, except decade, which we treated as a numeric variable that starts at zero. All

256 models were run separately for body mass and head-body length (Table S2).

257   We used a set of global models that included fixed effects of MAT, MAP, sex, season

258 collected (spring, summer, fall, and winter), human population density, and the traits listed above

259 ('Mammal traits'). Inclusion of traits as fixed effects allowed us to model variation in traits

260 associated with size across the mammalian body size spectrum (e.g., Smith et al. 2004). To

261 model how these same traits mediate body size variation in specific climate contexts and how

262 effects of urbanization change across climate contexts, we also examined the interactions of

263 MAT x human population density, MAT x hibernation, MAT x habitat buffering, MAT x

264 small/large mammals, population density x diurnal/nocturnal, and population density x

265 small/large mammals. We included three random intercepts of ecoregion, decade, and species

266 (Table S2).

267   After running each global model, we used backward stepwise selection with the step

268 function in the R package *lmerTest* (Kuznetsova et al. 2017) to find the best-fit model. We

269 checked residuals of the final models, minus the random effect of decade (due to matrix

270 complexity), and found no evidence of spatial autocorrelation (Fig. S3). Marginal and

271 conditional R^2s were obtained for the best-fit models using the R package *MuMIn* (Barton 2012).

272   To account for potential effects of evolutionary history in these models, we re-ran the

273 best-fit body mass and head-body length models using phylogenetic generalized linear mixed

274 models (PGLMMs) using the R package *phyr* (Li et al. 2020). PGLMM and LMM results were

275 largely concordant (Table S3), thus only LMM results are presented in the main text.

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RESULTS

278 Aggregation of data across multiple sources, generated a significant dataset to examine spatially-

279 structured changes in mammal body mass and head-body length in relation to climate, human

280 population density, and a key life history traits. The top model of body mass variation included

281 the following covariates: Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP),

282 season, sex, human population density, all traits, and all interactions besides population density x

283 small/large mammals (Marginal $R^2 = 0.36$, Conditional $R^2 = 0.98$). Significant main effects

284 include MAT, MAP, season, sex, human population density, hibernation, and small/large mean

285 binned body mass (Table 1a). This model also included strong interactive effects between MAT,

286 population density, and traits. The negative interaction between MAT and population density

287 implies that while mammal body mass increases with decreasing MAT in general, this trend is

288 much stronger in areas with higher densities of humans ($\beta = -0.003$, $p < 0.001$; Table 1a, Fig. 2).

289   Traits strongly mediated responses of body mass to climate and urbanization. With

290 increasing MAT, species that hibernate decrease in body mass, whereas non-hibernators increase

291 in body mass ($\beta = -0.021$, $p < 0.001$; Table 1a, Fig. 3A). Buffered and non-buffered species

292 decrease in body mass with increasing MAT, but the strength of the decrease is stronger for

293 buffered species ($\beta = -0.018$, $p < 0.001$; Table 1a, Fig. 3B). Diurnal species are larger in body

294 mass and decrease in mass with increasing population density ($\beta = -0.014$, $p < 0.001$; Table 1a,

295 Fig. 3C), compared to nocturnal species or those scored as "both" (Table 1a, Fig. 3C). Both large

296 and small mammals (binned mean size) decrease in body mass with increasing MAT, but the

297 strength of the decrease is stronger for larger species ($\beta = 0.023$, $p < 0.001$; Table 1a, Fig. 3D).

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298   When examining head-body length as a body size metric, the best-fit model consisted of

299   MAT, MAP, season, population density, all traits, and all interactions except MAT x human

300   population density (Marginal R^2 = 0.50, Conditional R^2 = 0.98). Significant single predictors are

301   MAP, season, human population density, hibernation, and small/large mean binned head-body

302   length (Table 1b). MAT is not significant in the top spatial models on its own, but is important

303   when conditioned by traits. There is a strong main effect of increasing head-body length with

304   increasing human population density (β = 0.009, $p < 0.001$; Table 1b).

305   Similar to body mass, we find strong interactive effects between MAT and population

306   density with traits. Head-body length is negatively correlated with MAT for species that

307   hibernate, but positively correlated with MAT for non-hibernators (β = -0.008, $p < 0.001$; Table

308   1b, Fig. 3E). Species that utilize habitat buffering decrease in head-body length with increasing

309   MAT at a faster rate than non-buffered species (β = -0.004, $p < 0.001$; Table 1b, Fig. 3F). Both

310   diurnal (β = -0.007, $p < 0.001$;) and nocturnal (β = -0.009, $p < 0.001$; Table 1b, Fig. 3G) species

311   decrease in head-body length with increasing population density, whereas species that display

312   both tendencies increase in head-body length with increasing population density. The effect of

313   the decrease in head-body length with increasing MAT is stronger for larger mammals compared

314   to smaller species (β = 0.005, $p < 0.001$; Table 1b, Fig. 3H). Small mammals decrease slightly

315   with increasing population density, while large mammals increase in head-body length with

316   increasing population density (β = -0.003, $p < 0.001$; Table 1b, Fig. 3I).

317

318   **<u>DISCUSSION</u>**

319   Climate as a driver of animal body size change has been well documented across both space and

320   time (Smith et al. 1995; Gardner et al. 2011; Sheridan & Bickford 2011). However, a myriad of

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321   anthropogenic global changes (e.g., habitat degradation and fragmentation, pollution,

322   overpopulation) can also impact organisms at both local and regional scales, promoting complex

323   responses that may be difficult to contextualize with regard to longstanding ecogeographic rules.

324   Further, these responses likely vary among species and clades because life history traits mediate

325   exposure and thus the intensity of changing conditions. Here, we investigate how climate (a more

326   constant global change driver over earth history) and urbanization (a novel disturbance)

327   influence mammalian body size, and how life history traits mediate those effects. We test these

328   ideas by utilizing hundreds of thousands of compiled mammal body size records from natural

329   history collections and field censuses, spanning 80 years and over 100 North American species.

330   Despite nearly two centuries of work examining the links between climate and body size,

331   we found urbanization is more tightly linked with changes in body size compared to temperature.

332   Finding weak support for interspecific Bergmann's Rule, Gohli and Voje (2016) suggested that

333   other variables, besides temperature and latitude, are more important drivers of mammalian body

334   mass; however, few studies have tested broad-scale effects of urbanization on body size across

335   mammal species. In all cases, the main effect of increased urbanization was larger body size,

336   consistent with mammals benefiting from increased food resources, nutritionally poor diets,

337   ecological release (i.e., from predators and competitors), or all three (Babinska-Werka 1981;

338   Tomassini et al. 2014; Brown et al. 2017; Santini et al. 2019; but see Nielsen et al. 2013).

339   Conversely, we found no clear evidence for urban heat island effects on body size. We had

340   considered that interactions between climate and urbanization could mean that heat island effects

341   might only be present in the coldest areas. But here as well, we found the opposite - mammals in

342   urbanized, cold areas have larger, not smaller, body masses than their rural counterparts, a result

343   that likely speaks to more available food in urban areas. While a few studies have found support

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344 for urban heat island effects leading to reductions in body size in ectotherms (Merckx et al. 2018;

345 Dahirel et al. 2019), there is currently no evidence of mammals following this trend. The overall

346 result across all mammals examined is that head-body lengths are greater in urban areas

347 regardless of temperature. Our study does not account for intra-urban variation in land use that

348 can influence heat island pockets (e.g., Hart & Sailor 2009); as such, fine-scale investigations of

349 the relationship between surface characteristics with temperature and body size may more

350 precisely demonstrate the role of heat islands in impacting body size.

351   Our results suggest that one key outcome of urbanization is provisioning of novel,

352 reliable food resources. Yom-Tov (2003) found a similar result for carnivoran body size;

353 increased body size was related to increased anthropogenic food sources and not temperature. In

354 addition to increased food, cities provide reliable water resources and shelter by use of built

355 structures, which might decrease energetic costs and benefit growth rate and body condition

356 (Bateman & Fleming 2012). The one exception to this pattern is that body mass was lightest in

357 the warmest, most urbanized areas. It is possible that predictable food resources in urban settings

358 results in low starvation risk (Lima 1986; Cuthill et al. 2000), or that a temperature threshold

359 exists above which increased body size becomes less energetically advantageous (regardless of

360 available food). This pattern may also emerge if constant food availability permits survival in

361 milder winters where fat reserves are less critical, potentially also aiding quicker locomotor

362 movements to escape predation or reductions in foraging time (Metcalfe & Ure 1995; Kullberg et

363 al. 1996; Downes 2001; Macleod et al. 2005). Future studies quantifying food availability

364 between spatially distinct regions is warranted as some mammals appear to be adapting to novel

365 food resources in urbanized areas (e.g., Harris & Munshi-South 2017).

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366   We acknowledge that some species may be urbanophobic or unable to exploit resources

367   provided in urban areas. Our strict filtering criteria limited our analyses to abundant and well

368   collected mammal species, but these species are likely to be urbanophilic or urban-neutral given

369   that many collections are near human-populated areas. Thus, our combined results do not

370   necessarily apply to all North American mammal species, and it is known that the percentage of

371   urbanized area plays a role in determining which species occupy those areas (Ordeñana et al.

372   2010). Ultimately, life history strategies as well as morphological traits facilitate the ability to

373   occupy urban environments, and filter out species lacking suitable characteristics (Croci et al.

374   2008; Jokimäki et al. 2016; Jung & Threlfall 2018). Thus, species inhabiting the most urbanized

375   areas are likely those with suites of traits that allow utilization of the novel resources in cities.

376   Even so, Parsons et al. (2018) found no difference in species diversity or richness along an

377   urban-wild gradient, and suggested mammals likely adapted to developed areas over the last few

378   decades. Further studies investigating species occupancy across developed gradients will help

379   elucidate adaptive trait responses to human-dominated landscapes.

380   Species traits directly related to thermoregulation and energetics appear to play an

381   integral role in mediating the effects of climate and urbanization on body size, but not in the

382   directions we predicted from theory. We predicted species that utilize thermal buffering (habitat

383   buffering and hibernation) would show weaker responses of body size change with warming

384   temperatures as these traits allow for avoidance of unfavorable climatic conditions (Fuller et. al.

385   2016). In contrast, we found species that use these behaviors are more sensitive to warming

386   temperatures than non-buffered species, and respond to warming temperatures with stronger

387   decreases in body size. Thus, for hibernators, exposure to temperatures during the active season

388   alone may still represent a sufficiently strong selective pressure. For species with thermal

389   buffering, lack of sufficient microhabitat heterogeneity due to extreme climates, clearcutting of

390   forests, or increases in forest fires can result in decreased variation in ambient temperatures

391   between exposed and buffered areas and ultimately reduce the effectiveness of that behavior

392   (Huey et al. 2012; Suggitt et al. 2018). Another unexpected result relates to our finding of an

393   increase in body size for non-hibernating mammals. Further work to better understand

394   physiological tolerances for thermal buffering species in relation to patterns of global change are

395   necessary. These relationships may be complex and involve multiway interactions between

396   landscape change, climate change, and species traits.

397   Daily activity pattern represents another important trait for adaptation to changing

398   environments. Flexibility in activity times appears to be advantageous in more urbanized areas.

399   McCain and King (2014) found mammals that can switch between diurnality and nocturnality

400   were least likely to respond negatively or respond at all to climate change, and postulated this

401   was due to the ability of these species to select climatic conditions that are suitable for activities.

402   Relative to mammals that are flexible in their activity times, we found diurnal species decrease in

403   body size with increasing urbanization. Decreases in body size may represent an adaptation to

404   avoid predation, including human detection (i.e. crypsis; Stankowich & Campbell 2016;

405   Guralnick et al. 2020). With increasing urbanization, nocturnal mammals also decreased in head-

406   body length, but increased in mass in relation to species that are active anytime. Decreases in

407   head-body length are also suggestive of an adaptive response to avoid detection, while increasing

408   mass is indicative of nocturnal mammals benefiting from increased food resources in urban

409   areas. The same idea may hold for species that are able to selectively avoid human detection by

410   being flexible in activity times.

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411   Finally, our results provide new insight into average body size itself as a trait that can

412   modulate responses to changing environments. With warming temperatures, we found larger

413   mammals are decreasing at a faster rate than smaller mammals. This result is in contrast to the

414   meta-analysis of Ashton et al. (2000), who found no difference between small or large mammals.

415   However, a reanalysis of that dataset demonstrated no general tendency for small mammals to

416   increase or decrease in size, while larger mammals tended to display a Bergmann's-like response

417   (Freckleton et al. 2003), consistent with our results. In another meta-analysis of 73 North

418   American mammal species, McCain and King (2014) found the largest mammals examined were

419   27 times more likely to respond to climate change compared to the smallest mammals. These

420   previous studies are all limited in that they are meta-analyses (also see Nengovhela et al. 2020),

421   vary in statistical approach, and do not leverage the dense intraspecific sampling we achieved

422   here. Our work draws strength from the use of a single hierarchical modeling framework for

423   separate measures of body mass and head-body length and reveals a robust signal of larger

424   mammals being more sensitive to changes in temperature, and conforming to Bergmann's Rule.

425   Lastly, small or large size does not mediate changes in body mass with increasing urbanization;

426   however, we did find large mammals increase in head-body length, while small mammals

427   decrease slightly. These results do not lend support to the Island Rule, where we would expect

428   body size homogenization with increasing urbanization (Schmidt & Jenson 2003). Instead,

429   increasing length for larger species may aid movement across fragmented landscapes (Merckx et

430   al. 2018).

431   In this work, we have focused primarily on the utility of digital biodiversity datasets such

432   as natural history collections and ecological monitoring efforts to examine spatial trends in

433   mammal body size. However, we recognize that temporal changes may also be inherent given

18

434 well-known climate and urbanization changes over the timescale of our dataset. We explicitly fit

435 a decadal random term to control for this variation, but the constituent datasets themselves are

436 also temporally structured, complicating issues with controlling for methodological issues

437 (Guralnick et al. 2020). One future possibility is to add a spatially controlled time-series, which

438 would provide a strong basis for examining temporal trends across multiple sites. In addition,

439 finer-scale regional or community-level ecological studies would provide a more detailed

440 understanding of the drivers of temporal changes (Ohlberger 2013).

441   Our understanding of how human-mediated pressures impact mammalian body size has

442 remained limited for decades, and is often tied to simplistic ecogeographic "rules", whose

443 validity continues to be called into question (Reimer et al. 2018). Our data-intensive work

444 showcases the importance of incorporating other human disturbances beyond climate change,

445 and also reflects how multiple pressures interact with species traits to influence change in body

446 size. Beyond the finding that urbanization had a strong impact on body size, it was surprising

447 that species with climate buffering traits were more sensitive to temperature. This has major

448 implications for management of native species and suggests that these species may be under

449 increasingly intense selection not just for life history parameters such as phenology, but also

450 morphological traits like body size. Further collection and digitization of trait data remains

451 essential for improved understanding of large-scale spatiotemporal patterns of body size change,

452 especially given accelerating climate warming and urbanization (Grimm et al. 2008; Seto et al.

453 2012; Christensen et al. 2013).

454

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462 **REFERENCES**

463 Alroy, J. (2001). A multispecies overkill simulation of the end- Pleistocene megafaunal mass
464 extinction. *Science*, 292, 1893–1896.
465
466 Ashton, K.G., Tracy, M.C. & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals?
467 *Am. Nat.*, 156, 390–415.
468
469 Babinska-Werka, J. (1981). Food of the striped field mouse in different types of urban areas.
470 *Acta Theriol.*, 26, 285–299.
471
472 Barton, K. (2012). Package 'MuMIn'. Model selection and model averaging based on
473 information criteria. R package version 3.2.4. http://cran.r-project.org/web/packages/MuMIn/
474 index.html.
475
476 Bateman, P.W. & Fleming, P.A. (2012). Big city life: carnivores in urban environments. *J. Zool.*,
477 287, 1–23.
478
479 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models
480 using Eigen and S4. R package version 1.1-7.
481
482 Beckmann, J.P. & Berger, J. (2003). Using black bears to test ideal-free distribution models
483 experimentally. *J. Mammal.*, 84, 594–606.
484
485 Bergmann, C. (1847). About the relationships between heat conservation and body size of
486 animals. *Goett. Stud.* (original in German), 1, 595–708.
487
488 Blackburn, T.M. & Hawkins, B.A. (2004). Bergmann's rule and the mammal fauna of northern
489 North America. *Ecography*, 27, 715–724.
490
491 Brown, James H. (1995). Macroecology. University of Chicago Press.
492
493 Brown, J.H. & Maurer, B.A. (1986). Body size, ecological dominance and Cope's rule. *Nature*,
494 324, 248–250.

495

496 Brown, J.H., Marquet, P.A. & Taper, M.L. (1993). Evolution of body size: consequences of an
497 energetic definition of fitness. *Am. Nat.*, 142, 573–584.

498

499 Brown, J.S., Kotler, B.P. & Porter, W.P. (2017). How foraging allometries are resource
500 dynamics could explain Bergmann's rule and the body-size diet relationship in mammals. *Oikos*,
501 126, 224–230.

502

503 Calhoun, J.B. (1943). North American census of small mammals. Release no. 1. Announcement
504 of program. Rodent ecology program. Johns Hopkins University Pres.

505

506 Calhoun, J.B. (1949). North American census of small mammals. Release no. 2. Annual report of
507 census made in 1948. Rodent ecology program. Johns Hopkins University Press.

508

509 Calhoun, J.B. (1950). North American census of small mammals. Release no. 3. Annual report of
510 census made in 1949. Roscoe B. Jackson Memorial Laboratory.

511

512 Calhoun, J.B. (1951). North American census of small mammals. Release no. 4. Annual report of
513 census made in 1950. Roscoe B. Jackson Memorial Laboratory.

514

515 Calhoun, J.B. (1956). Population dynamics of vertebrates. Compilations of research data.
516 Release no. 5. 1951 Annual report - North American census of small mammals. U.S. Department
517 of Health, Education, and Welfare, Public Health Service, National Institute of Mental Health.

518

519 Calhoun, J.B. & Arata, A.A. (1957a). Population dynamics of vertebrates. Compilations of
520 research data. Release no. 6. 1952 Annual report - North American census of small mammals.
521 U.S. Department of Health, Education, and Welfare, Public Health Service, National Institute of
522 Mental Health.

523

524 Calhoun, J.B. & Arata, A.A. (1957b). Population dynamics of vertebrates. Compilations of
525 research data. Release no. 7. 1953 Annual report - North American census of small mammals.
526 U.S. Department of Health, Education, and Welfare, Public Health Service, National Institute of
527 Mental Health.

528

529 Calhoun, J.B. & Arata, A.A. (1957c). Population dynamics of vertebrates. Compilations of
530 research data. Release no. 8. 1954 Annual report - North American census of small mammals.
531 U.S. Department of Health, Education, and Welfare, Public Health Service, National Institute of
532 Mental Health.

533

534 Calhoun, J.B. & Arata, A.A. (1957d). Population dynamics of vertebrates. Compilations of
535 research data. Release no. 9. 1955 and 1956 Annual report - North American census of small
536 mammals and certain summaries for the years 1948–1956. U.S. Department of Health,
537 Education, and Welfare, Public Health Service, National Institute of Mental Health.

538

539   Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Biminda- Emonds, O.R.P., Sechrest, W.,
540   Orme, C.D.L. & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal
541   species. *Science*, 309, 1239–1241.
542
543   Chapman, A.D. & Wieczorek, J. (2006). Guide to best practices for georeferencing. Global
544   Biodiversity Information Facility.
545
546   Christensen, J.H. *et al.* (2013). Climate Phenomena and their Relevance for Future Regional
547   Climate Change in Climate Change 2013: The Physical Science Basis. *Contribution of Working*
548   *Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* 1–6,
549   pp. 1217–1308.
550
551   Croci, S., Butet, A. & Clergeau, P. (2008). Does urbanization filter birds on the basis of their
552   biological traits? *Condor*, 110, 223–240.
553
554   Cuthill, I.C., Maddocks, S.A., Weall, C.V. & Jones, E.K.M. (2000). Body mass regulation in
555   response to changes in feeding predictability and overnight energy expenditure. *Behav. Ecol.*, 11,
556   189–195.
557
558   Dahirel, M., De Cock, M., Vantieghem, P. & Bonte, D. (2019). Urbanization-driven changes in
559   web building and body size in an orb web spider. *J. Anim. Ecol.*, 88, 79–91.
560
561   Downes, S. (2001). Trading heat and food for safety: costs of predator avoidance in a lizard.
562   *Ecology*, 82, 2870–2881.
563
564   Fang, Y. & Jawitz, J.W. (2018). High-resolution reconstruction of the United States human
565   population distribution, 1790 to 2010. *Sci. Data*, 5, 180067.
566
567   Fischer, J.D., Cleeton, S.H., Lyons, T.P., Miller, J.R. (2012). Urbanization and the Predation
568   Paradox: The Role of Trophic Dynamics in Structuring Vertebrate Communities. *Bioscience*, 62,
569   809–818.
570
571   Freckleton, R.P., Harvey, P.H. & Pagel, M. (2003). Bergmann's rule and body size in mammals.
572   *Am. Nat.*, 161, 821–825.
573
574   Fuller, A., Mitchell, D., Maloney, S.K. & Hetem, R.S. (2016). Towards a mechanistic
575   understanding of the responses of large terrestrial mammals to heat and aridity associated with
576   climate change. *Clim. Change Resp.*, 3, 10.
577
578   Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011). Declining body size:
579   a third universal response to warming? *Trends Ecol. Evol.*, 26, 285–291.
580
581   Gohli, J. & Voje, K.L. (2016). An interspecific assessment of Bergmann's rule in 22 mammalian
582   families. *BMC Evolutionary Biology*, 16, 222.
583
584   Gould, S.J. (1966). Allometry and size in ontogeny and phylogeny. *Biol. Rev.*, 41, 587–638.

22

585

586 Grimm, N. B. et al. (2008). Global change and the ecology of cities. *Science*, 319, 756–760.

587

588 Guralnick, R. & Constable, H. (2010). VertNet: creating a data-sharing community. *Bioscience*,
589 60, 258–259.

590

591 Guralnick, R.P. *et al.* (2016). The Importance of digitized biocollections as a source of trait data
592 and a new VertNet resource. *Database*, 2016, baw158.

593

594 Guralnick, R., Hantak, M.M., Li, D. & McLean, B.S. (2020). Body size trends in response to
595 climate and urbanization in the widespread North American deer mouse, *Peromyscus*
596 *maniculatus*. *Sci. Rep.*, 10, 8882.

597

598 Harris, S.E. & Munshi-South, J. (2017). Signatures of positive selection and local adaptation to
599 urbanization in white-footed mice (*Peromyscus leucopus*). *Mol. Ecol.*, 26, 6336–6350.

600

601 Hart, M.A. & Sailor, D. J. (2009). Quantifying the influence of land-use and surface
602 characteristics on spatial variability in the urban heat island. *Theor. Appl. Climatol.*, 95, 397–
603 406.

604

605 Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E.
606 (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology
607 and adaptation. *Philos. Trans. R. Soc. B*, 367, 1665–1679.

608

609 Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrard, G. E., Bekessy, S.A.,
610 Fuller, R.A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L. E. & Kendal, D. (2016). Cities are
611 hotspots for threatened species. *Glob. Ecol. Biogeogr.*, 25, 117–126.

612

613 Johnson, G.E. (1931). Hibernation in mammals. *Q. Rev. Biol.*, 6, 439–461.

614

615 Jokimäki, J., Suhonen, J., Jokimäki-Kaisanlahti, M.-L. & Carbó-Ramirez, P. (2016). Effects of
616 urbanization on breeding birds in European towns: Impacts of species traits. *Urban Ecosyst.*, 19,
617 1565–1577.

618

619 Jung, K. & Threlfall, C.G. (2018). Trait-dependent tolerance of bats to urbanization: a global
620 meta-analysis. *Proc. R. Soc. B Biol. Sci.*, 285, 20181222.

621

622 Kullberg, C., Fransson, T. & Jakobsson, S. (1996). Impaired predator evasion in fat blackcaps
623 (*Sylvia atricapilla*). *Proc. R. Soc. B Biol. Sci.*, 263, 1671–1675.

624

625 Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B. (2017). lmerTest Package: Tests in Linear
626 Mixed Effects Models. *J. Stat. Softw.*, 82, 1–26.

627

628 Laney, C. & Lunch, C. (2019). neonUtilities: utilities for working with NEON data. R package
629 version 1.3.1. https://cran.r-project.org/web/packages/neonUtilities.

630

23

631 Li D., Dinnage R., Helmus M. & Ives A. (2020). phyr: An R package for phylogenetic species–
632 distribution modelling in ecological communities. *Methods Ecol. Evol.*, doi.org/10.1111/2041-
633 210X.13471.

635 Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: determinants of body
636 mass in birds. *Ecology*, 67, 377–385.

638 Lindstedt, S. L. & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in
639 mammals. *Am. Nat.*, 125, 873–878.

641 Macleod, R., Gosler, A.G. & Cresswell, W. (2005). Diurnal mass gain strategies and perceived
642 predation risk in the great tit *Parus major*. *J. Anim. Ecol.*, 74, 956–964.

644 McCain, C.M. & King, S.R.B. (2014). Body size and activity times mediate mammalian
645 responses to climate change. *Glob. Change Biol.*, 20, 1760–1769.

647 McKinney, M.L. (2008). Effects of urbanization on species richness: a review of plants and
648 animals. *Urban Ecosyst.*, 11, 161–176.

650 McNab, B.K. (1980). Food habits, energetics, and the population biology of mammals. *Am. Nat.*,
651 116, 106–124.

653 McNab, B.K. (2010). Geographic and temporal correlations of mammalian size reconsidered: a
654 resource rule. *Oecologia*, 164, 13–23.

656 Meiri, S. & Dayan, T. (2003). On the validity of Bergmann's rule. J. *Biogeogr.,* 30, 331–351.

658 Merckx, T., Kaiser, A. & Van Dyck, H. (2018). Increased body size along urbanization gradients
659 at both community and intraspecific level in macro-moths. *Glob. Change Biol.*, 24, 3837–3848.

661 Metcalfe, N.B. & Ure, S.E. (1995). Diurnal variation in flight performance and hence potential
662 predation risk in small birds. *Proc. R. Soc. B Biol. Sci.*, 261, 395–400.

664 National Ecological Observatory Network. (2019). Data Products: DP1.10072.001. Provisional
665 data downloaded from http://data.neonscience.org on May 10, 2019. Battelle, Boulder, CO,
666 USA.

668 Naya, D.E., Naya, H. & Cook, J. (2017). Climate change and body size trends in aquatic and
669 terrestrial endotherms: does habitat matter? *PLoS ONE*, 12, e0183051.

671 Nengovhela, A., Denys, C. & Taylor, P.J. (2020). Life history and habitat do not mediate
672 temporal changes in body size due to climate warming in rodents. *PeerJ*, 8, 9792.

674 Nielsen, S.E., Cattet, M.R.L., Boulanger, J., Cranston, J., McDermid, G.J., Shafer, A.B.A. &
675 Stenhouse, G.B. (2013). Environmental, biological and anthropogenic effects on grizzly bear
676 body size: temporal and spatial considerations. *BMC Ecology*, 13, 31.

24

677

678 Ohlberger, J. (2013). Climate warming and ectotherm body size – from individual physiology to
679 community ecology. *Funct. Ecol.*, 27, 991–1001.

680

681 Oke, T.R. (1882). The energetic basis of the urban heat island. *Q. J. R. Meteorol. Soc.*, 108, 1–
682 24.

683

684 Ordeñana, M.A., Crooks, K.R., Boydston, E.E., Fisher, R.N., Lyren, L.M., Siudyla, S., Haas,
685 C.D., Harris, S., Hathaway, S.A., Turschak, G.M., Miles, A.K. & Van Vuren, D.H. (2010).
686 Effects of urbanization on carnivore species distribution and richness. J. *Mammal*, 91, 1322–
687 1331.

688

689 Parsons, A.W., Forrester, T., Baker-Whatton, M.C., McShea, W., Rota, C.T., Schuttler, S.G.,
690 Millspaugh, J. & Kays, R. (2018). Mammal communities are larger and more diverse in
691 moderately developed areas. *eLife*, 7, e38012.

692 Pergams, O.R.W. & Lacy, R.C. (2008) Rapid morphological and genetic change in Chicago-area
693 *Peromyscus*. *Mol Ecol.*, 17, 450–463.

694 Pineda-Munoz, S., Evans, A. & Alroy, J. (2016). The relationship between diet and body mass in
695 terrestrial mammals. *Paleobiology*, 42, 659–669.

696

697 PRISM Climate Group. (2020). PRISM climate data. Available at https://prism.oregonstate.edu.
698 R Core Team. (2018). R: a language and environment for statistical computing. R Foundation for
699 Statistical Computing. https://www.R-project.org/.

700

701 Rapacciuolo, G., Marin, J., Costa, G.C., Helmus, M.R., Behm, J.E., Brooks, T.M., Hedges, S.B.,
702 Radeloff, V.C., Young, B.E. & Graham, C.H. (2017). The signature of human pressure history
703 on the biogeography of body mass in tetrapods. *Global Ecol. Biogeogr.*, 26, 1022–1034.

704

705 Riemer, K., Guralnick, R.P. & White, E.P. (2018). No general relationship between mass and
706 temperature in endothermic species. *elife*, 7, e27166.

707

708 Robinette, W.L., Baer, C.H., Pillmore, R.E. & Knittle, C.E. (1973). Effects of nutritional change
709 on captive mule deer. *J. Wildl. Manage*, 37, 312–326.

710

711 Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A. &
712 Ancillotto, L. (2019). One strategy does not fit all: Determinants of urban adaptation in
713 mammals. *Ecol. Lett.*, *22*, 365–376.

714

715 Scheffers, B.R., Edward, D.P., Diesmos, A., William, S.E. & Evans, T.A. (2014). Microhabitats
716 reduce animal's exposure to climate extremes. *Glob. Change Biol.*, 20, 495–503.

717

718 Schmidt, N.M. & Jensen, P.M. (2003). Changes in mammalian body length over 175 years –
719 adaptations to a fragmented landscape? *Conserv. Ecol.*, 72, 6.

720

25

721 Schmidt, N.M. & Jensen, P.M. (2005). Concomitant patterns in avian and mammalian body
722 length changes in Denmark. *Ecol. Soc.*, 10, 5.
723
724 Seto, K.C., Güneralp, B. & Hutyra, L.R. (2012). Global forecasts of urban expansion to 2030 and
725 direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. USA*, 109, 16083–16088.
726
727 Sheridan, J.A. & Bickford, D. (2011). Shrinking body size as an ecological response to climate
728 change. *Nat. Clim. Change*, 1, 401–406.
729
730 Smith, F.A., Betancourt, J.L. & Brown, J.H. (1995). Evolution of body size in the woodrat over
731 the past 25,000 years of climate change. *Science*, 270, 2012–2014.
732
733 Smith, F.A., Brown, J.H., Alroy, J., Charnov, E.L., Haskell, J.P., Dayan, T., Lyons, S.K.,
734 Enquist, B.J., Ernest, S.K.M., Hadly, E.A., Jones, K.E., Kaufman, D.M., Marquet, P.A., Maurer,
735 B.A., Niklas, K.J., Porter, W.P., Tiffney, B.H. & Willig, M.R. (2004). Similarity of mammalian
736 body size across the taxonomic hierarchy and across space and time. *Am. Nat.*, 163, 672–691.
737
738 Stankowich, T. & Campbell, L.A. (2016). Living in the danger zone: exposure to predators and
739 the evolution of spines and body armor in mammals. *Evolution*, 70, 1501–1511.
740
741 Suggitt, A.J., Wilson, R.J., Isaac, N.J.B., Beale, C.M., Auffret, A.G., August, T., Bennie, J.J.,
742 Crick, H.Q.P., Duffield, S., Fox, R., Hopkins, J.J., Macgregor, N.A., Morecroft, M.D., Walker,
743 K.J. & Maclean, I.M.D. (2018). Extinction risk from climate change is reduced by microclimatic
744 buffering. *Nat. Clim. Change*, 8, 713–717.
745
746 Terrien, J., Perret, M. & Aujard, F. (2011). Behavioral thermoregulation in mammals: a review.
747 *Front. Biosci.*, 16, 1428–1444.
748
749 Tiwari, V. & Kashikar, A. (2019). OutlierDetection: Outlier Detection. R package version 0.1.1.
750 https://cran.r-project.org/web/packages/OutlierDetection/index.html.
751
752 Tomassini, A., Colangelo, P., Agnelli, P., Jones, G. & Russo, D. (2014). Cranial size has
753 increased over 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or
754 urbanization? *J. Biogeogr.*, 41, 944–953.
755
756 Upham, N.S., Esselstyn, J.A. & Jetz, W. (2019). Inferring the mammal tree: species-level sets of
757 phylogenies for questions in ecology, evolution, and conservation. *PLOS Biol.*, 17, e3000494.
758
759 Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P.,
760 Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016). Global Human
761 Footprint maps for 1993 and 2009. *Sci. Data*, 3, 10067.

762 Weeks, B.C., Willard, D.E., Zimova, M., Ellis, A.A., Witynski, M.L., Hennen, M. & Winger,
763 B.M. (2020). Shared morphological consequences of global warming in North American
764 migratory birds. *Ecol. Lett.*, 23, 316–325.

765 Wieczorek, J., Guo, Q., Boureau, C. & Wieczorek, C. (2001). Georeferencing calculator.
766 http://manisnet.org/gci2.html.

767

768 Yom-Tov, Y. (2003). Body sizes of carnivores commensal with humans have increased over the
769 past 50 years. *Funct. Ecol.*, 17, 323–327.

770

771

772

773

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TABLES

794   Table 1. Top (A) body mass and (B) head-body (HB) length model results. Bold effects are

795   significant.

Term	Estimate	Std. Error	p-value
(A)*Body mass*			
Intercept	**3.446**	**0.156**	**<0.001**
MAT	**-0.014**	**0.003**	**<0.001**
MAP	**-0.001**	**0.000**	**0.001**
Season:spring	**0.025**	**0.001**	**<0.001**
Season:summer	**0.013**	**0.001**	**<0.001**
Season:winter	**-0.007**	**0.001**	**<0.001**
Sex:male	**0.002**	**0.000**	**<0.001**
Population density	**0.008**	**0.001**	**<0.001**
Hibernation:yes	**-0.359**	**0.121**	**0.004**
Buffered:yes	-0.012	0.111	0.917
Diurnal/nocturnal:diurnal	0.343	0.175	0.053
Diurnal/nocturnal:nocturnal	-0.013	0.145	0.931
Small/large body mass:small	**-1.838**	**0.123**	**<0.001**
MAT x small/large body mass:small	**0.023**	**0.003**	**<0.001**
MAT x population density	**-0.003**	**0.000**	**<0.001**
MAT x hibernation:yes	**-0.021**	**0.001**	**<0.001**
MAT x buffered:yes	**-0.018**	**0.001**	**<0.001**
Population density x diurnal/nocturnal:diurnal	**-0.014**	**0.001**	**<0.001**
Population density x diurnal/nocturnal:nocturnal	**-0.002**	**0.001**	**0.003**
(B)*HB length*			
Intercept	**2.677**	**0.052**	**<0.001**
MAT	-0.001	0.001	0.115
MAP	**-0.001**	**0.000**	**0.007**
Season:spring	**0.008**	**0.000**	**<0.001**
Season:summer	**0.002**	**0.000**	**<0.001**
Season:winter	0.000	0.000	0.433
Population density	**0.009**	**0.001**	**<0.001**
Hibernation:yes	**-0.141**	**0.041**	**0.001**
Buffered:yes	-0.052	0.037	0.166
Diurnal/nocturnal:diurnal	0.075	0.059	0.205
Diurnal/nocturnal:nocturnal	-0.047	0.049	0.340
Small/large HB length:small	**-0.587**	**0.041**	**<0.001**
MAT x small/large HB length:small	**0.005**	**0.001**	**<0.001**
Population density x small/large HB length:small	**-0.003**	**0.001**	**<0.001**
MAT x hibernation:yes	**-0.008**	**0.000**	**<0.001**
MAT x buffered:yes	**-0.004**	**0.001**	**<0.001**
Population density x diurnal/nocturnal:diurnal	**-0.007**	**0.001**	**<0.001**

Population density x diurnal/nocturnal:nocturnal	-0.009	0.000	<0.001

FIGURE LEGENDS

Fig. 1. Body mass and HB length record localities. Designated spatial ecoregions are colored and the key shows the total number of body mass and head-body (HB) length records from each ecoregion.

Fig. 2. Mammalian body mass is influenced by the interaction between human population density and mean annual temperature. In colder and more urbanized areas mammal body mass is the heaviest, while in the warmest areas that experience the highest levels of urbanization, body mass is the lightest.

Fig. 3. Mammalian body mass is influenced by the interaction between (A) hibernation and mean annual temperature; (B) habitat buffering and mean annual temperature; (C) activity time (diurnal/nocturnal) and human population density; (D) and large/small size and mean annual temperature. Mammalian head-body (HB) length is influenced by the interaction between (E) hibernation and mean annual temperature; (F) habitat buffering and mean annual temperature; (G) activity time (diurnal/nocturnal) and human population density; (H) large/small size and mean annual temperature, and (I) large/small size and human population density.
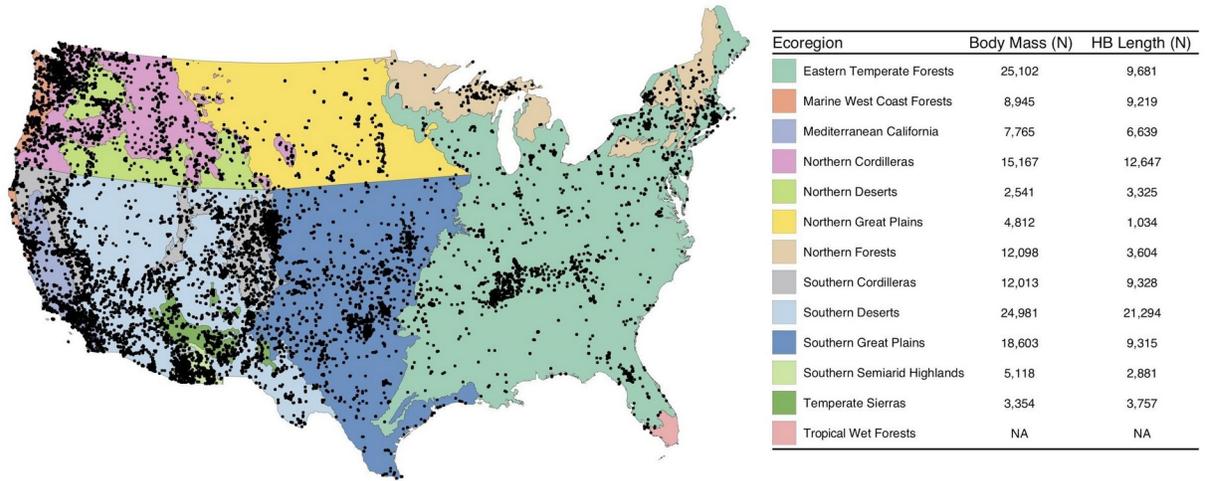
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819 **<u>FIGURES</u>**

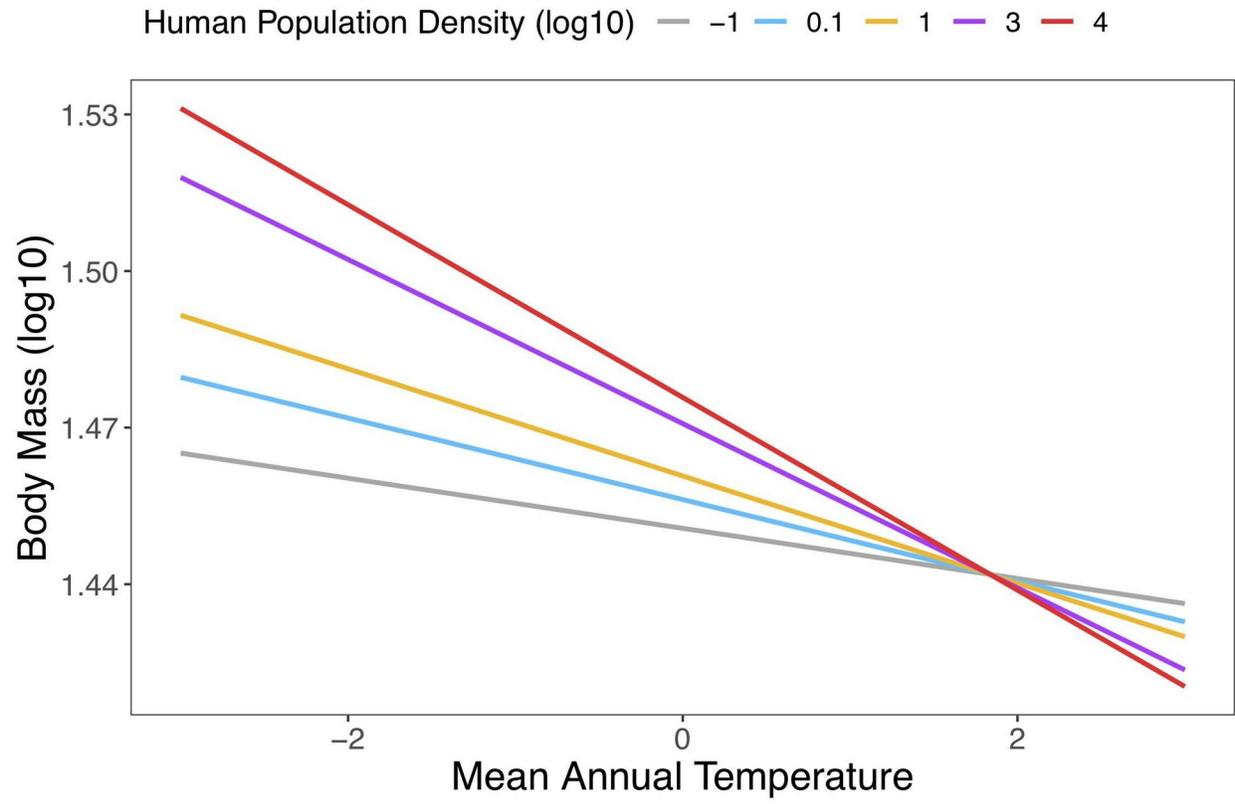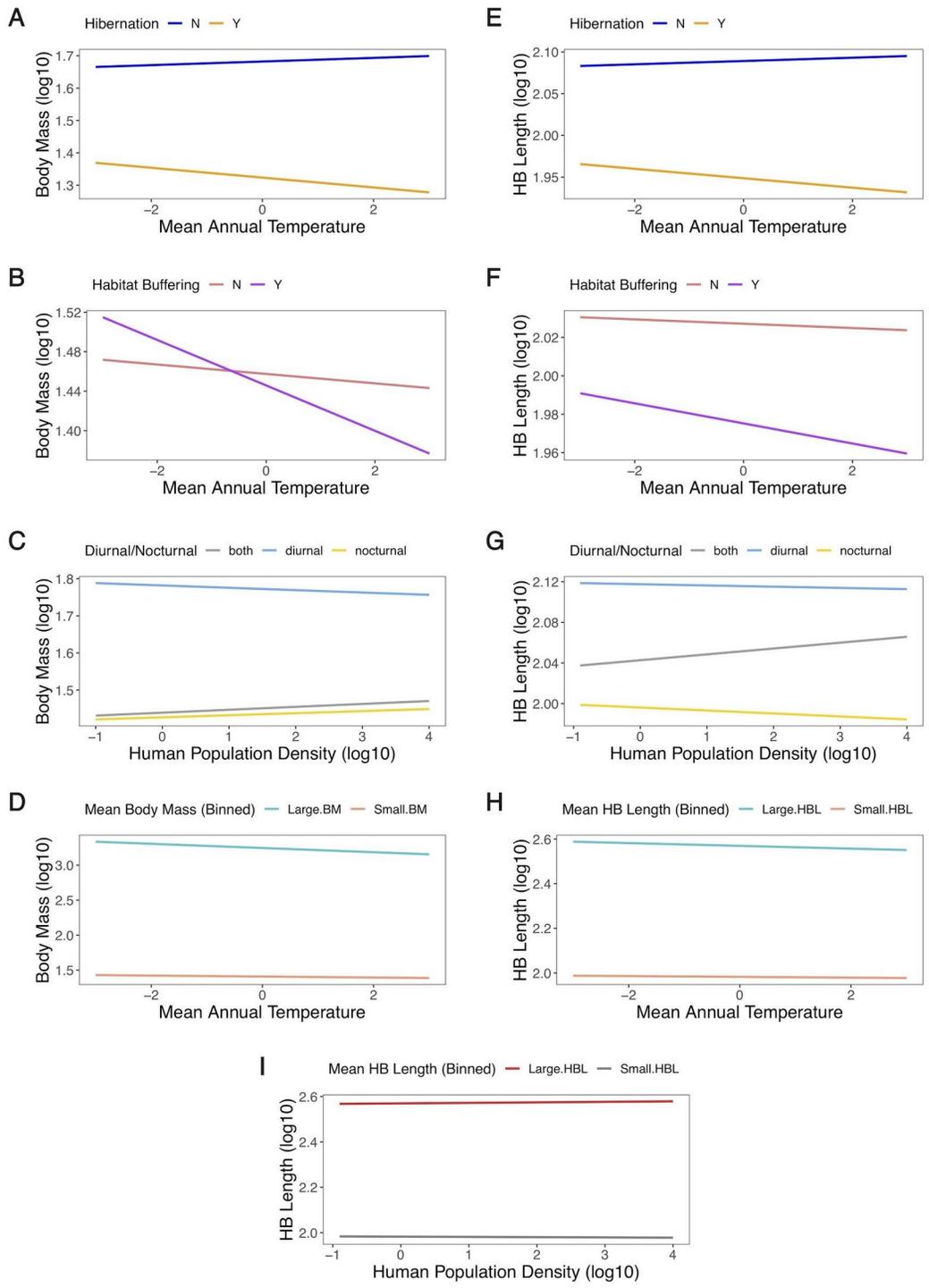| Ecoregion	Body Mass (N)	HB Length (N)
Eastern Temperate Forests	25,102	9,681
Marine West Coast Forests	8,945	9,219
Mediterranean California	7,765	6,639
Northern Cordilleras	15,167	12,647
Northern Deserts	2,541	3,325
Northern Great Plains	4,812	1,034
Northern Forests	12,098	3,604
Southern Cordilleras	12,013	9,328
Southern Deserts	24,981	21,294
Southern Great Plains	18,603	9,315
Southern Semiarid Highlands	5,118	2,881
Temperate Sierras	3,354	3,757
Tropical Wet Forests	NA	NA

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821
822 Fig. 1.
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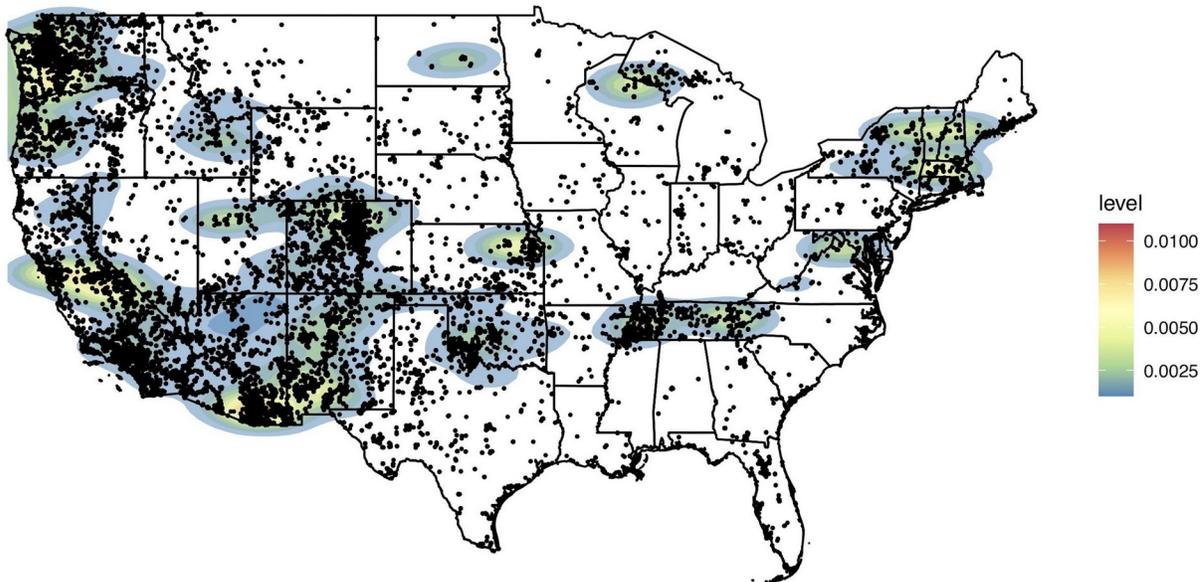827
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833   Fig. 2.
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836 Fig. 3.
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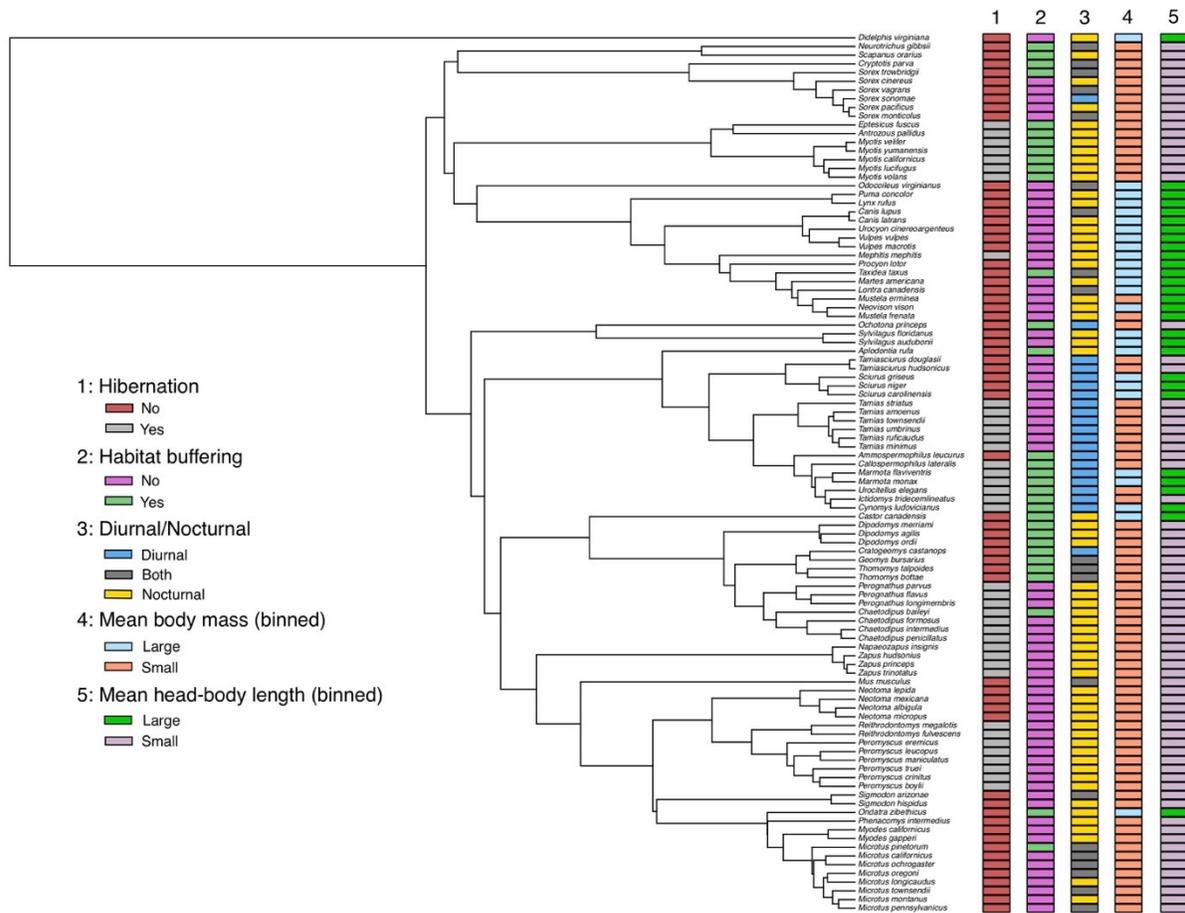
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SUPPLEMENTAL FIGURES

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844   Fig. S1. Heat map of mammal record densities.

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850   Fig. S2. Phylogeny of study species trimmed from the tree of Upham et al. (2019;
851   http://vertlife.org/data/mammals/) including traits used in this study. Hibernating species include
852   those that experience daily torpor or more prolonged hibernation bouts. Mammals that utilize
853   habitat buffering include species that are fossorial, volant, and subterranean, while non-buffered
854   species in our study are terrestrial and arboreal. Species with a large mean body size are >500g;
855   >200mm, while small species are <500g; <200mm. Subset phylogenies of species in separate
856   body mass and head-body length data datasets were used in the PGLMM analyses.
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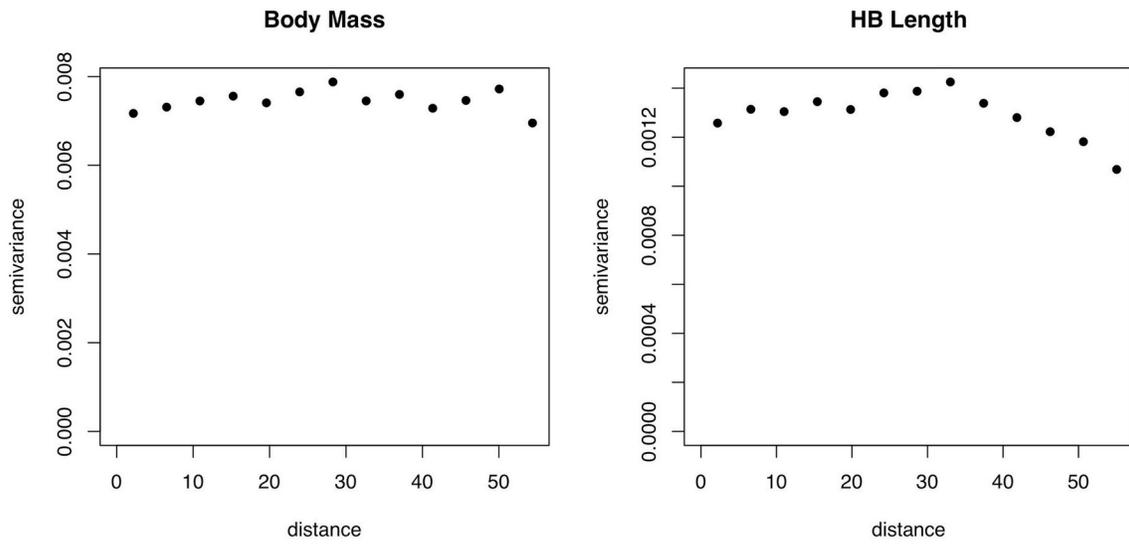
Body Mass

HB Length

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860 Fig. S3. Spatial autocorrelation residuals of the final body mass and head-body (HB) length
861 models.
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SUPPLEMENTAL TABLES

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878 Table S1. Body mass, total length, tail length, and head-body (HB) length ranges extracted from
879 the literature. R2 values are based on regressions of $\log_{10}$ head-body length and $\log_{10}$ body mass
880 for each species.

Species	Mass range (g)	Total length range (mm)	Tail length range (mm)	HB length range (mm)	R2 (mass-length)	References
Ammospermophilus leucurus	94-118	188-240			0.03	1,2
Antrozous pallidus	13-30		30-60		0.07	1
Aplodontia rufa	700-1400	290-500	9-40		0.47	1,3,4,5
Callospermophilus lateralis	120-395	225-305	65-120		0.39	1
Canis latrans	7000-33940	1000-1600	200-450		0.36	1,6
Canis lupus	23000-80000	1000-1800	150-600	700-1400	0.13	1,7
Castor canadensis	13000-32000	900-1200			0.46	1
Chaetodipus baileyi	21-45	170-245		60-115	0.25	1,8
Chaetodipus formosus	10.5-26	75-215	80-120		0.21	1,9
Chaetodipus intermedius	8-20	156-190	80-112		0.21	1
Chaetodipus penicillatus	10-27	145-205	65-120	60-100	0.32	1,10
Cratogeomys castanops	180-415	220-315			0.51	1,11,12
Cryptotis parva	2.8-6.5	63-92		40-80	0.13	1
Cynomys ludovicianus	615-1675	330-450			0.04	1,13
Didelphis virginiana	1750-6000	330-915			0.19	1,14
Dipodomys agilis	50-87	232-320	130-200	100-135	0.46	15,16,17
Dipodomys merriami	35-55	150-250	78-155	65-122	0.09	1
Dipodomys ordii	50-95	200-365	90-175		0.25	1,18
Eptesicus fuscus	10-30	100-130	30-55		0.14	1,19
Geomys bursarius	250-470	180-360	45-110		0.29	1,20
Ictidomys tridecemlineatus	90-170	200-310	30-105		0.03	1,21
Lontra canadensis	5000-14000	800-1400	300-600	500-900	0.11	1,22
Lynx rufus	4000-15000	650-1050		500-1000	0.33	1,23
Marmota flaviventris	1450-5220	430-700			0.54	1,24
Marmota monax	1820-6000	400-685			0.21	1,25
Martes americana	200-1600	300-700		250-700	0.38	1,26
Mephitis mephitis	700-6300	400-800			0.50	1
Microtus californicus	25-85	125-220	30-75		0.58	1,27
Microtus longicaudus	20-85	140-250	30-105	75-155	0.66	1,28
Microtus montanus	33-90	125-220		80-150	0.33	29
Microtus ochrogaster	25-70	120-180		85-140	0.49	1,30
Microtus oregoni	11.5-34	120-160			0.33	31
Microtus pennsylvanicus	28-70	120-200		80-150	0.38	1,32
Microtus pinetorum	15-40	78-125	10-40		0.45	1,33
Microtus townsendii	42-95	150-235	40-82		0.61	1,34
Mus musculus	10-35	60-105	50-105		0.73	1
Mustela erminea	25-230	150-400		120-280	0.76	1,35
Mustela frenata	70-500	200-500		155-310	0.73	1
Myodes californicus	13-40			80-120	0.61	1
Myodes gapperi	6-45	95-190		55-140	0.62	1
Myotis californicus	2.5-6	65-100	22-45		0.00	1

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Myotis lucifugus	4-14.5	65-102	22-65	35-70	0.11	1
Myotis velifer	4.7-17			42-67	0.11	1
Myotis volans	5-10.5	80-110	30-55		0.00	1
Myotis yumanensis	4-8	65-100	25-45		0.07	1
Napaeozapus insignis	15-35	200-260			0.39	1,36
Neotoma albigula	120-300	215-400		75-300	0.34	1,37
Neotoma lepida	95-350	200-415			0.38	1,38
Neotoma mexicana	125-250	250-430	90-185	130-210	0.24	1,39
Neotoma micropus	150-360	280-400	90-175	150-240	0.55	1,40
Neovison vison	400-1700	415-700		290-505	0.53	1
Neurotrichus gibbsii	7-15.5	95-135			0.08	1
Ochotona princeps	118-220	140-220			0.01	1,41
Odocoileus virginianus	30000-150000	1400-2100			0.29	1,42
Ondatra zibethicus	500-1800	400-620		180-400	0.35	1,43
Perognathus flavus	5-12	85-150		45-75	0.16	1,44
Perognathus longimembris	5.5-11	95-160	30-100	45-85	0.20	45,46,47
Perognathus parvus	13-30			60-95	0.21	1,48
Peromyscus boylii	17-45	150-230	50-125		0.25	1
Peromyscus crinitus	11-27	145-202			0.41	1,49
Peromyscus eremicus	15-35		60-140	70-110	0.25	1
Peromyscus leucopus	13-40	120-205			0.44	1,50
Peromyscus maniculatus	9-35	90-228		43-130	0.45	1
Peromyscus truei	15-35	140-240		50-117	0.36	1,51
Phenacomys intermedius	18-55	120-160			0.40	1,52
Procyon lotor	1500-10900	560-1000	150-500	300-700	0.63	1,53
Puma concolor	28000-120000			860-1540	0.29	1
Reithrodontomys fulvescens	9.7-20	117-190		50-100	0.18	1,54
Reithrodontomys megalotis	6.5-23	112-175		50-100	0.34	1,55
Scapanus orarius	50-90	130-180			0.08	1,56
Sciurus carolinensis	300-770	380-530		190-305	0.44	1
Sciurus griseus	350-1000	450-630			0.24	1,57
Sciurus niger	530-1000	420-700			0.10	1,58
Sigmodon arizonae	110-230	180-360		125-190	0.36	1,59
Sigmodon hispidus	65-235	210-370		100-210	0.49	1,60
Sorex cinereus	2.2-6	80-135	20-55	30-125	0.27	1,61
Sorex monticolus	4-11.5	90-160	17-70	40-100	0.37	1
Sorex pacificus	4.8-18	105-160			0.65	62
Sorex sonomae	7.5-17			62-92	0.43	1,63
Sorex trowbridgii	3.7-8	85-140		40-90	0.19	64,65
Sorex vagrans	3-8.5	78-130		40-82	0.36	66,67
Sylvilagus audubonii	705-1200	270-450		250-402	0.05	1,68
Sylvilagus floridanus	800-1550	325-480			0.16	1
Tamias amoenus	25-80	175-250			0.48	1,69
Tamias minimus	37-63	175-235	65-120		0.25	1
Tamias ruficaudus	50-75			117-150	0.30	1,70
Tamias striatus	65-127	210-270		123-170	0.31	1
Tamias townsendii	55-125	190-300	50-150		0.17	1,71
Tamias umbrinus	42-80	190-250		100-145	0.28	1

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Tamiasciurus douglasii	135-315	250-355	80-160		0.50	1
Tamiasciurus hudsonicus	165-310	265-390	75-175		0.53	1
Taxidea taxus	3600-12000	500-900			0.40	1,72
Thomomys bottae	70-210	150-300	36-92		0.60	1
Thomomys talpoides	60-160	158-260		105-180	0.55	1,73
Urocitellus elegans	235-435		45-95	170-280	0.10	1
Urocyon cinereoargenteus	2000-9000	800-1125	200-600		0.24	1,74
Vulpes macrotis	1600-3075		250-400	400-600	0.10	1,75
Vulpes vulpes	3000-14000		300-600	455-800	0.21	1,76
Zapus hudsonius	13-30	150-245	90-165	55-110	0.29	1,77
Zapus princeps	18-42	200-260	100-165		0.38	1,78
Zapus trinotatus	14-37	210-265	100-167		0.43	1

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897 Table S2. Full linear mixed-effects models (LMM) that were used to test for variation in (A)
898 body mass and (B) head-body length across spatial scales.

Models

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A: Body Mass

mod1 <- lmer(body_mass ~ MAT + MAP + season + sex + pop_density + hibernation + buffered + diurnal_nocturnal + mean_body_mass_binned + MAT:pop_density + MAT:hibernation + MAT:buffered + pop_density:diurnal_nocturnal + MAT:mean_body_mass_binned + pop_density:mean_body_mass_binned + (1 | ecoregion) + (1 | species) + (1 | decade)

B: Head-body Length

mod2 <- lmer(HB_length ~ MAT + MAP + season + sex + pop_density + hibernation + buffered + diurnal_nocturnal + mean_HB_length_binned + MAT:pop_density + MAT:hibernation + MAT:buffered + pop_density:diurnal_nocturnal + MAT:mean_HB_length_binned + pop_density:mean_HB_length_binned + (1 | ecoregion) + (1 | species) + (1 | decade)

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914 Table S3. Top (A) body mass and (B) head-body (HB) length PGLMM model results. Bold
915 effects are significant.

Term	Value	lower CI	upper CI
(A)*Body mass*			
Intercept	**6.897**	**6.273**	**7.515**
MAT	**-0.033**	**-0.045**	**-0.021**

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MAP	**-0.003**	**-0.005**	**-0.001**
Season:spring	**0.058**	**0.055**	**0.062**
Season:summer	**0.029**	**0.027**	**0.032**
Season:winter	**-0.015**	**-0.019**	**-0.011**
Sex:male	**0.006**	**0.003**	**0.008**
Population density	**0.018**	**0.015**	**0.021**
Hibernation:yes	**-0.922**	**-1.715**	**-0.129**
Buffered:yes	0.225	-0.378	0.826
Diurnal/nocturnal:diurnal	0.395	-0.251	1.040
Diurnal/nocturnal:nocturnal	-0.275	-0.604	0.052
Small/large body mass:small	**-2.583**	**-3.112**	**-2.049**
MAT x small/large body mass:small	**0.054**	**0.041**	**0.066**
MAT x population density	**-0.006**	**-0.008**	**-0.005**
MAT x hibernation:yes	**-0.048**	**-0.052**	**-0.044**
MAT x buffered:yes	**-0.042**	**-0.048**	**-0.036**
Population density x diurnal/nocturnal:diurnal	**-0.033**	**-0.039**	**-0.027**
Population density x diurnal/nocturnal:nocturnal	**-0.005**	**-0.009**	**-0.002**
(B)*HB length*			
Intercept	**5.732**	**5.490**	**5.973**
MAT	**-0.006**	**-0.011**	**-0.002**
MAP	**-0.001**	**-0.002**	**0.000**
Season:spring	**0.018**	**0.017**	**0.020**
Season:summer	**0.005**	**0.004**	**0.007**
Season:winter	-0.001	-0.003	0.001
Population density	**0.019**	**0.016**	**0.022**
Hibernation:yes	**-0.366**	**-0.659**	**-0.074**
Buffered:yes	0.029	-0.191	0.249
Diurnal/nocturnal:diurnal	0.108	-0.114	0.330
Diurnal/nocturnal:nocturnal	**-0.099**	**-0.207**	**0.010**
Small/large HB length:small	**-0.786**	**-1.015**	**-0.558**
MAT x small/large HB length:small	**0.014**	**0.009**	**0.018**
Population density x small/large HB length:small	**-0.006**	**-0.009**	**-0.003**
MAT x hibernation:yes	**-0.018**	**-0.020**	**-0.016**
MAT x buffered:yes	**-0.009**	**-0.012**	**-0.007**
Population density x diurnal/nocturnal:diurnal	**-0.016**	**-0.019**	**-0.013**
Population density x diurnal/nocturnal:nocturnal	**-0.020**	**-0.021**	**-0.018**

Supplemental References

1. Myers, P., Espinosa, R., Parr, C.S., Jones, T., Hammond, G.S. & Dewey, T.A. (2015). The animal diversity web. See http://animaldiversity.ummz.umich.edu (accessed 22 August 2020).

2. Belk, M.C. & Smith, H.D. (1991). *Ammospermophilus leucurus*. Mammalian Species, 368, 1–8.

927 3. Carraway, L.N. & Verts, B.J. (1993). *Aplodontia rufa*. Mammalian Species, 431, 1–10.
928
929 4. Lovejoy, B.P. & Black, H.C. (1974). Growth and weight of the mountain beaver, *Aplodontia*
930 *rufa pacifica*. Journal of Mammalogy, 55, 364–369.
931
932 5. Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (2003). Wild mammals of North America:
933 biology, management, and conservation. Baltimore, MD: Johns Hopkins University Press.
934
935 6. Bekoff, M. (1977). *Canis latrans*. Mammalian Species, 79, 1–9.
936
937 7. Mech, L.D. (1974). *Canis lupus*. Mammalian Species, 37, 1–6.
938
939 8. Paulson, D.D. (1988). *Chaetodipus baileyi*. Mammalian Species 297, 1–5.
940
941 9. Jameson, E.W., Jr., & H.J. Peeters. (2004). Mammals of California. University of California
942 Press, Berkeley, USA.
943
944 10. Ziv, Y. & Smallwood, J.A. (2000). Gerbils and heteromyids – interspecific competition and
945 the spatio-temporal niche. In Activity Patterns in Small Mammals: An Ecological Approach (eds.
946 S. Halle and N. C. Stenseth), pp. 159–176. Ecological Studies, Springer Verlag.
947
948 11. Davidow-Henry, B.R., Jones, J.K. Jr., Hollander, R.R. (1989). *Cratogeomys castanops*.
949 Mammalian Species, 338, 1–6.
950
951 12. Hedgal, P.L., Ward, A.L., Johnson, A.M. & Tietjen, H.P. (1965). Notes on the life history of
952 the Mexican pocket gopher (*Cratogeomys castanops*). J Mammal., 46:334–335.
953
954 13. Hoogland, J.L. (1996). *Cynomys ludovicianus*. Mammalian Species, 535, 1–10.
955
956 14. McManus, J.J. (1974). *Didelphis virginiana*. Mammalian Species, 40, 1–6.
957
958 15. Price, M.V., Longland, W.S., Goldingay, R.L., (1991). Niche relationships of *Dipodomys*
959 *agilis* and *D. stephensi*: two sympatric kangaroo rats of similar size. American Midland
960 Naturalist, 126, 172–186.
961
962 16. Bleich, V.C., Price, M.V. (1995). Aggressive behavior of *Dipodomys stephensi*, an
963 endangered species, and *Dipodomys agilis*, a sympatric congener. J Mammal., 76, 646–651.
964
965 17. Wolff, J.O., Sherman, P.W. (2007). Rodent Societies: An Ecological and Evolutionary
966 Perspective. University of Chicago Press, Chicago, Illinois.
967
968 18. Garrison, T.E. & Best, T.L. (1990). *Dipodomys ordii*. Mammalian Species, 353, 1–10.
969
970 19. Kurta, A. & Baker, R.H. (1990). *Eptesicus fuscus*. Mammalian Species, 356, 1–10.
971
972 20. Connior, M.B. (2011). *Geomys bursarius*. Mammalian Species, 43, 104–117.

41

973

974   21. Streubel, D.P. & Fitzgerald, J.P. (1978). *Gulo gulo*. Mammalian Species, 103, 1–5.

975

976   22. Larivière, S. & Walton, L.R. (1998). *Lontra canadensis*. Mammalian Species, 587, 1–8.

977

978   23. Larivière, S. & Walton, L.R. (1997). *Lynx rufus*. Mammalian Species, 563, 1–8.

979

980   24. Frase, B.A. & Hoffmann, R.S. (1980). *Marmota flaviventris*. Mammalian Species, 135, 1–8.

981

982   25. Kwiecinski, G.G. (1998). *Marmota monax*. Mammalian Species, 591, 1–8.

983

984   26. Clark, T.W., Anderson, E., Douglas, C. & Strickland, M. (1987). *Martes americana*.
985   Mammalian Species, 289, 1–8.

986

987   27. Cudworth, N.L. & Koprowski, J.L. (2010). *Microtus californicus* (Rodentia: Cricetidae).
988   Mammalian Species, 42, 230–243.

989

990   28. Smolen, M.J. & Keller, B.L. (1987). *Microtus longicaudus*. Mammalian Species, 271, 1–7.

991

992   29. Sera, W.E. & Early, C.N. (2003). *Microtus montanus*. Mammalian Species, 716, 1–10.

993

994   30. Stalling, D.T. (1990). *Microtus ochrogaster*. Mammalian Species, 355, 1–9.

995

996   31. Carraway, L.N. & Verts, B.J. (1985). *Microtus oregoni*. Mammalian Species, 233, 1–6.

997

998   32. Reich, L.M. (1981). *Microtus pennsylvanicus*. Mammalian Species, 159, 1–8.

999

1000   33. Smolen, M.J. (1981). *Microtus pinetorum*. Mammalian Species, 147, 1–7.

1001

1002   34. Cornely, J.E. & Verts, B.J. (1988). *Microtus townsendii*. Mammalian Species, 325, 1–9.

1003

1004   35. King, C.M. (1983). *Mustela erminea*. Mammalian Species, 195, 1–8.

1005

1006   36. Whitaker, J.O. Jr. & Wrigley, R.E. (1972). *Napaeozapus insignis*. Mammalian Species, 14,
1007   1–6.

1008

1009   37. Macêdo, R.H. & Mares, M.A. (1988). *Neotoma albigula*. Mammalian Species, 310, 1–7.

1010

1011   38. Verts, B.J. & Carraway, L.N. (2002). *Neotoma lepida*. Mammalian Species, 699, 1–12.

1012

1013   39. Cornely, J.E. & Baker, R.J. (1986). *Neotoma mexicana*. Mammalian Species, 262, 1–7.

1014

1015   40. Braun, J.K. & Mares, M.A. (1989). *Neotoma micropus*. Mammalian Species, 330, 1–9.

1016

1017   41. Smith, A.T. & Weston, M.L. (1990). *Ochotona princeps*. Mammalian Species, 352, 1–8.

1018

1019   42. Smith, W.P. (1991). *Odocoileus virginianus*. Mammalian Species, 388, 1-13.
1020
1021   43. Willner, G.R., Feldhamer, G.A., Zueker, E.E. & Chapman, J.A. (1980). *Ondatra zibethicus*.
1022   Mammalian Species, 141, 1–8.
1023
1024   44. Best, T.L. & Skupski, M.P. (1994). *Perognathus flavus*. Mammalian Species, 471, 1–10.
1025
1026   45. Flake, L. & C.D. Jorgensen. (1969). Invasion of a "trapped out" southern Nevada habitat by
1027   *Perognathtis longimembris*. Great Basin Nat., 29, 143–149.
1028
1029   46. Bartholomew, G.A. & Cade, T.J. (1957). Temperature regulation, hibernation, and
1030   aestivation in the Little Pocket Mouse, *Perognathus longimembris*. Journal of Mammalogy, 38,
1031   60–72.
1032
1033   47. US Fish and Wildlife Service (USFWS). (2010). Pacific pocket mouse (*Perognathus
1034   longimembris pacificus*) 5-Year Review: Summary and Evaluation. Carlsbad Fish and Wildlife
1035   Office: Service USFW.
1036
1037   48. Verts, B.J. & Kirkland, G.L. Jr. (1988). *Perognathus parvus*. Mammalian Species, 318, 1–8.
1038
1039   49. Johnson, D.W. & Armstrong, D.M. (1987). *Peromyscus crinitus*. Mammalian Species, 287,
1040   1–8.
1041
1042   50. Lackey, J.A., Huckaby, D.G. & Ormiston, B.G. (1985). *Peromyscus leucopus*. Mammalian
1043   Species, 247, 1–10.
1044
1045   51. Hoffmeister, D.F. (1981). *Peromyscus truei*. Mammalian Species, 161, 1–5.
1046
1047   52. McAllister, J.A. & Hoffmann, R.S. (1988). *Phenacomys intermedius*. Mammalian Species,
1048   305, 1–8.
1049
1050   53. Lotze, J.-H. & Anderson, S. (1979). *Procyon lotor*. Mammalian Species, 119, 1–8.
1051
1052   54. Spencer, S.R. & Cameron, G.N. (1982). *Reithrodontomys fulvescens*. Mammalian Species,
1053   174, 1–7.
1054
1055   55. Webster, W.D. & Jones, J.K. Jr. (1982) *Reithrodontomys megalotis*. Mammalian Species,
1056   167, 1–5.
1057
1058   56. Hartman, G.D. & Yates, T.L. (1985). *Scapanus orarius*. Mammalian Species, 253, 1–5.
1059
1060   57. Carraway, L.N. & Verts, B.J. (1994). *Sciurus griseus*. Mammalian Species, 474, 1–7.
1061
1062   58. Koprowski, J.L. (1994). *Sciurus niger*. Mammalian Species, 479, 1–9.
1063

1064 59. Gwinn, R.N., Palmer, G.H., Koprowski, J.L. (2011). *Sigmodon arizonae*. Mammalian
1065 Species, 883, 149–154.
1066
1067 60. Cameron, G.N., & Spencer, S.R. (1981). *Sigmodon hispidus*. Mammalian Species, 158, 1–9.
1068
1069 61. Whitaker, J.O. Jr. (2004). *Sorex cinereus*. Mammalian Species, 743, 1–9.
1070
1071 62. Carraway, L.N. (1985). *Sorex pacificus*. Mammalian Species, 231, 1–5.
1072
1073 63. Reid, F.A. (2006). A Field Guide to Mammals of North America North of Mexico. Houghton
1074 Mifflin, Boston.
1075
1076 64. George, S.B. (1989). *Sorex trowbridgii*. Mammalian Species, 337, 1–5.
1077
1078 65. Lomolino, M.V., Perault, D.R. (2007). Body size variation of mammals in a fragmented,
1079 temperate rainforest. Conserv. Biol., 21, 1059–1069.
1080
1081 66. Gillihan, S.W. & Foresman, K.R. (2004). *Sorex vagrans*. Mammalian Species, 744, 1–5.
1082
1083 67. Clothier, R.R. (1955). Contribution to the life history of *Sorex vagrans* in Montana. J.
1084 Mamm., 36, 214–221.
1085
1086 68. Chapman, J.A. & Willner, G.R. (1978). *Sylvilagus audubonii*. Mammalian Species, 106, 1–4.
1087
1088 69. Sutton, D.A. (1992). *Tamias amoenus*. Mammalian Species, 390, 1–8.
1089
1090 70. Best, T.L. (1993). *Tamias ruficaudus*. Mammalian Species, 452, 1–7.
1091
1092 71. Sutton, D.A. (1993). *Tamias townsendii*. Mammalian Species, 435, 1–6.
1093
1094 72. Long, C.A. (1973). *Taxidea taxus*. Mammalian Species, 26, 1–4.
1095
1096 73. Verts, B.J. & Carraway, L.N. (1999). *Thomomys talpoides*. Mammalian Species, 618, 1–11.
1097
1098 74. Fritzell, E.K. & Haroldson, K.J. (1982). *Urocyon cinereoargenteus*. Mammalian Species,
1099 189, 1–8.
1100
1101 75. McGrew, J.C. (1979). *Vulpes macrotis*. Mammalian Species, 123, 1–6.
1102
1103 76. Larivière, S. & Pasitschniak-Arts, M. (1996). *Vulpes vulpes*. Mammalian Species, 537, 1–11.
1104
1105 77. Whitaker, J.O. Jr. (1972). *Zapus hudsonius*. Mammalian Species, 11, 1–7.
1106
1107 78. Hart, E.B., Belk, M.C., Jordan, E., Gonzalez, M.W. (2004). *Zapus princeps*. Mammalian
1108 Species, 749, 1–7.
1109

1110