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Miami heat: Urban heat islands influence the thermal suitability of habitats for ectotherms

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16 **ABSTRACT**

17 The urban heat island effect, where urban areas exhibit higher temperatures than less-developed

18 suburban and natural habitats, occurs in cities across the globe and is well understood from a

19 physical perspective and at broad spatial scales. However, very little is known about how thermal

20 variation caused by urbanization influences the ability of organisms to live in cities. Ectotherms

21 are sensitive to environmental changes that affect thermal conditions, and therefore increased

22 urban temperatures may pose significant challenges to thermoregulation and alter temperature-

23 dependent activity. To evaluate whether these changes to the thermal environment affect the

24 persistence and dispersal of ectothermic species in urban areas, we studied two species of *Anolis*

25 lizards (*A. cristatellus* and *A. sagrei*) introduced to Miami-Dade County, FL, USA, where they

26 occur in both urban and natural habitats. We calculated canopy openness and measured operative

27 temperature (T_e), which estimates the distribution of body temperatures in a non-

28 thermoregulating population, in four urban and four natural sites. We also captured lizards

29 throughout the day and recorded their internal body temperature (T_b). We found that urban areas

30 had more open canopies and higher T_e compared to natural habitats. Lab trials showed that *A.*

31 *cristatellus* preferred lower temperatures than *A. sagrei*. Urban sites currently occupied by each

32 species appear to lower thermoregulatory costs for both species, but only *A. sagrei* had field T_b

33 that were more often within their preferred temperature range in urban habitats compared to

34 natural areas. Furthermore, based on available T_e within each species' preferred temperature

35 range, urban sites with only *A. sagrei* appear less suitable for *A. cristatellus*, whereas natural

36 sites with only *A. cristatellus* are less suitable for *A. sagrei*. These results highlight how the

37 thermal properties of urban areas contribute to patterns of persistence and dispersal, particularly

38 relevant for studying species invasions worldwide.

39

INTRODUCTION

Habitat fragmentation and local-scale habitat modifications associated with urbanization

have profound effects on air and surface temperatures in cities. This phenomenon is called the

urban heat island effect, in which urban and developed areas are warmer and temporally more

variable than less developed and nearby natural habitats (Imhoff, Zhang, Wolfe, & Bounoua,

2010; Rizwan, Dennis, & Liu, 2008; Streutker, 2002). When humans construct and expand cities,

vegetative cover is reduced and replaced with impervious, heat-absorbing artificial surfaces such

as roads, parking lots, and buildings (Forman, 2014; Oke, 1982; Yuan & Bauer, 2007). At larger

scales, once-continuous habitats become fragmented with increased surface area exposed to solar

radiation (Delgado, Arroyo, Arévalo, & Fernández-Palacios, 2007; Mcdonald, Kareiva, &

Forman, 2008). At smaller scales, the distribution of warm and cool microclimates is highly

variable in cities, being influenced by diverse factors such as the placement of single trees and

the socio-economic status of the neighborhood (Georgi & Zafiriadis, 2006; Jenerette et al., 2007;

Kolbe et al., 2016). Thus urbanization drastically alters thermal environments in cities compared

to natural habitats, such as forests. Although the urban heat island effect is well studied from the

perspective of its physical characteristics, very little is known about the consequences for

organisms that inhabit cities (but see Angilletta et al., 2007). For ectothermic organisms in

particular, whether the altered distribution of thermal microhabitats and increased temperatures

of urban areas affect field body temperatures and related traits is an open question.

Environmental temperature increases in urban areas may have a direct impact on

ectotherm fitness. Enzymatic activity that drives metabolism, movement, reproduction, and

growth is usually positively correlated with body temperature up to an optimal functional

62   temperature, after which performance sharply decreases as temperature increases (Angilletta,

63   2009; Huey & Kingsolver, 1989). Activity rates, including mating and foraging, change

64   continuously with body temperature and reach their highest levels within the preferred

65   temperature range (Gunderson & Leal, 2015, 2016). Because maximal performance, such as

66   locomotion, can be critical for escaping predators, capturing prey, and defending territories

67   (Irschick & Losos, 1998), the environmental temperature can have a strong impact on fitness.

68   For example, when *Anolis* lizards were transplanted to a warmer habitat, those with maximal

69   performance at higher temperatures and greater performance breadth had a survival advantage

70   (Logan, Cox, & Calsbeek, 2014). Urban environments may be too extreme for some species,

71   with temperatures regularly above their thermal tolerances or lethal temperatures (Kappes,

72   Katzschner, & Nowak, 2012; Menke et al., 2011), and without enough cool refuges, some

73   species will be excluded from these areas. However, some ectotherms have been shown to have

74   increased thermal tolerance in cities; for example, urban ants in Sao Paulo, Brazil could tolerate

75   high temperatures (42°C) for longer than ants from rural areas (Angilletta et al., 2007).

76   Alternatively, if urban areas are warmer but temperatures are within physiological tolerances,

77   access to optimal and preferred body temperatures may increase, and constraints on activity time

78   and performance may be reduced (Gunderson & Leal, 2015). For example, shade from

79   landscaping vegetation increased activity time by nearly 400% for lizards in an arid ecosystem

80   (Ackley, Angilletta, DeNardo, Sullivan, & Wu, 2015). Whether increased urban temperatures

81   benefit or prove costly to organisms depends on how well ectotherms can use their habitat to

82   regulate body temperatures.

83   Thermoregulatory costs may change for ectotherms in urban areas where the vegetation

84   structure and thermal landscape (i.e., the spatial distribution of thermal microclimates) differ

85   significantly from natural habitats. To regulate their body temperatures, ectotherms exchange

86   heat with the surrounding environment (Angilletta, 2009), depending not only on ambient

87   conditions (e.g. air and ground temperatures, and access to solar radiation), but also the spatial

88   distribution of thermally variable microclimates (Sears & Angilletta, 2015; Sears, Raskin, &

89   Angilletta, 2011). Some ectothermic organisms actively thermoregulate, moving between cool

90   and warm microhabitats to achieve a preferred body temperature (Huey, Hertz, & Sinervo,

91   2003). Alternatively, the body temperature of an ectotherm in a thermally homogeneous habitat,

92   such as a dense forest, conforms to the ambient temperature (Huey et al., 2009). The costs of

93   each strategy, whether energetic (e.g. shuttling between basking sites) or opportunistic (e.g.

94   metabolic or performance losses when outside their preferred temperature range), depend on

95   both the amount of available sunny and shady microhabitats and their distribution in the habitat

96   (Huey & Slatkin, 1976; Sears et al., 2016; Sears & Angilletta, 2015). For example, a population

97   of *Anolis cristatellus* in warmer, more arid habitats in southwestern Puerto Rico actively

98   thermoregulates, whereas lizards in cooler forested habitats with fewer basking sites

99   thermoconform (Gunderson & Leal, 2012). Because the thermal landscape determines the

100   relative ease of achieving optimal and preferred temperatures (i.e., cost of thermoregulation)

101   (Sears et al., 2016), maximal performance capacity and activity time, which are important

102   proxies of fitness, could vary between habitats that differ in thermal quality. If warmer urban

103   areas are more favorable thermal environments, this may reduce thermoregulatory costs,

104   allowing organisms to expend less effort to reach preferred temperatures (Gunderson & Leal,

105   2012). Alternatively, thermoregulatory costs may increase if urban areas are too hot and

106   ectotherms spend more time and energy seeking cooler microhabitats (Lagarde et al., 2012;

107   Scheffers et al., 2013). Few studies have evaluated thermal ecology of ectotherms in cities, yet

108   this factor should strongly influence the ability of these organisms to persist in this widespread

109   and expanding type of environment.

110   Changes to the costs of temperature-dependent activity may influence the persistence of

111   ectotherms in cities and determine the ability of non-native ectothermic species to expand their

112   ranges. Due to habitat modification and extirpation of native species, among other urban

113   phenomena, urbanized areas can function as points of entry and centers of population growth for

114   introduced species (Blair & Johnson, 2008; Hufbauer et al., 2012). Furthermore, human activity

115   and land development often contribute positively to invasion success (Roura-Pascual et al., 2011;

116   Shochat et al., 2010). Because abiotic factors (e.g. temperature) play a major role in invasion

117   success (Menke & Holway, 2006), when the thermal qualities of an urban area benefit an

118   introduced species, such as those that prefer warmer conditions, urbanization may facilitate their

119   spread (Menke et al., 2011; Piano et al., 2017). Alternatively, urban temperatures may exceed

120   thermal tolerances, which may preclude introduced ectotherms from establishing in portions of

121   urban habitats (Kolbe et al., 2016). Because invasive species can cause environmental damage

122   and economic losses, understanding the mechanisms behind their spread and persistence is

123   critical (Zenni & Nuñez, 2013).

124   *Anolis* lizards are an excellent system for evaluating the impact of urbanization on

125   temperature-mediated traits in introduced species. Anoles have been used extensively in research

126   on thermoregulation (e.g. Hertz, Huey, & Stevenson, 1993; Huey et al., 2003; Huey, 1974).

127   Because of their relatively small size and small home ranges, their body temperatures can be

128   compared to nearby models that represent their body temperatures for a non-thermoregulating

129   population (i.e., the operative temperature: T_e), allowing for an assessment of habitat choice and

130   estimates of the costs of thermoregulation (Gunderson & Leal, 2012; Hertz, 1992; Huey et al.,

131 2003). The temperature dependence of locomotion (i.e., thermal performance curve or TPC) is

132 well-studied in anoles (Gunderson & Leal, 2012; Huey, Niewiarowski, Kaufmann, & Herron,

133 1989), and warmer conditions have been shown to impose selection on thermal performance in

134 anoles (Logan et al., 2014) as well as other lizard taxa (Gilbert & Miles, 2017). We studied the

135 effects of urban environments on the thermal biology of two species, *Anolis cristatellus* and

136 *Anolis sagrei*. Both species use similar portions of the structural habitat and are found in urban

137 and natural habitats in both their native and non-native ranges. Where they co-occur in the

138 Miami area, they have been shown to compete and affect each other's habitat use (Salzburg,

139 1984). *Anolis cristatellus* has lower reported thermal preferences and tolerances than *A. sagrei*,

140 and appears constrained to areas in Miami with high canopy cover (Corn, 1971; Kolbe et al.,

141 2016). *Anolis sagrei* is widespread throughout urban areas of Miami as well as some natural

142 forest locations (Battles, Moniz, & Kolbe, 2018).

143   We predict that the structural habitat changes because of urbanization will result in more

144 open canopies in urban compared to natural areas. We also predict that urban areas will be

145 warmer and more variable temporally than natural areas (T_e), demonstrating an urban heat island

146 effect at a scale relevant to lizards. Because thermal traits can acclimate or adapt to local

147 conditions (e.g. Clusella-Trullas & Chown, 2014), we predict that urban lizards in both species

148 will have higher thermal preferences (T_{pref}), higher optimal performance temperatures (T_{opt}), and

149 greater performance breadths than lizards from natural sites. Lizards may benefit in urban areas

150 if they can maintain T_b within their T_{pref} range for more time during the day compared to natural

151 areas. Alternatively, urban areas may present more extreme conditions (i.e., warmer overall and

152 fewer cool spots) than natural areas, reducing or eliminating these potential benefits. Finally, we

153 predict that the thermal characteristics, or thermal suitability, of a site largely dictate which of

154 the two species is present, lending support to the hypothesis that abiotic factors influence the

155 presence and spread of these invasive species.

156 **MATERIALS AND METHODS**

157 **Study species and study sites**

158   We studied two *Anolis* species, small insectivorous lizards found naturally in southern

159 North America, Central and South America, and throughout the Caribbean (Losos, 2009).

160 Several *Anolis* species have been introduced to the Miami metropolitan area (Kolbe et al., 2007),

161 two of which are common in both natural forest and urban areas (See S1 in supporting

162 information for density estimates). *Anolis sagrei* is native to Cuba and the Bahamas, and non-

163 native populations are now widely distributed in the southeastern United States with Miami area

164 populations dating to the 1940-60s (Bell, 1953; Kolbe et al., 2004). *Anolis cristatellus* is native

165 to Puerto Rico and was first documented in Miami in the mid-1970s (Bartlett & Bartlett, 1999;

166 Kolbe et al., 2007; Powell, Henderson, Adler, & Dundee, 1996; Wilson & Porras, 1983). In

167 contrast to the nearly ubiquitous *A. sagrei*, the distribution of *A. cristatellus* is more restricted,

168 radiating out from two independent points of introductions (Kolbe et al., 2016).

169   We conducted our study in four urban and four natural sites throughout the Miami

170 metropolitan area. Generally, natural sites were closed-canopy forests on upland hammocks,

171 consisting of hardwood-oak overstory canopy with palmettos and saplings in the understory. All

172 of the natural sites were forest patches within the urban matrix of metropolitan Miami. Urban

173 sites are located within human-altered areas, generally along roadsides with bike paths, canals,

174 and sidewalks. Sites vary in their intensity of urbanization with the Gables being the most urban.

175 We are unaware of any urban sites in Miami that contain only *A. cristatellus*. See S2 in

176 supporting information for map and photos of each site.

Operative Temperature

We measured operative temperature (T_e), the distribution of body temperatures in a non-thermoregulating population, which represents the available thermal environment for lizards. We made copper lizard models out of 28-gauge (0.32 mm) copper sheet, rolled into a cylinder and fitted with a cap from the same material on one end and flattened and folded to close the other end, and painted light brown to match lizard skin color and reflectance. Inside each model, we placed an iButton temperature logger (Thermochron model DS1921G-F5) that was wrapped in parafilm to increase waterproofing and then wrapped in cloth medical tape to buffer the iButton from directly touching the side of the model. The iButtons recorded temperatures every fifteen minutes for the duration of the study at each site. To place models at the natural sites, starting from near the center of the plot, we followed a random compass heading and distance and affixed a model on the nearest substrate at this location at a random height between 0 and 200 cm. This resulted in model placement on random orientations on tree trunks and branches, including underneath surfaces, where lizards regularly perch. In urban sites, we followed a transect parallel to the road, placing models evenly along the length of the transect at random heights between 0 and 200 cm, at a random distance from the road, and facing a random compass heading when on the substrate. At each site, we placed at least 30 operative temperature models. For all models, we recorded the substrate type and diameter of the vegetation. We calibrated the temperatures recorded by the models to more closely represent lizard T_b following Dzialowski (2005). We did this on sunny days from 08/28/2014 – 09/03/2014, which matched the weather conditions for days we collected data across all sites.

Body Temperature

While the models were deployed at a site, we captured lizards and recorded their internal body temperature (T_b) with a small thermocouple (K-type, 36-guage, 0.13 mm-diameter) briefly inserted into their cloaca. We captured lizards on days when the sun was out, providing lizards with the opportunity to thermoregulate. We captured 12 lizards (mixed males and females) per hour between 0700 and 1800, for a total of at least 132 lizards per site. At sites with both species (Red and Crandon), we captured 132 individuals of each species. We only captured undisturbed lizards, and never those that we observed moving between sun and shade patches (i.e. only those lizards not changing basking status). We did not resample individuals, ensured by marking captured lizards with a small dot placed on the body with white correctional fluid (WhiteOut). When it took more than one day to reach the sample size at a site, we only captured lizards when overall weather conditions were similar across sampling days. We sampled sites between June and August in 2014 (see S3 in supporting information for specific dates for each site).

Canopy Openness

We measured canopy openness by taking hemispherical photos facing upward from model locations and lizard capture locations with a handheld camera (10-megapixel Canon® Powershot SD1200 IS) and attached fish-eye lens. We analyzed these photos with Gap Light Analyzer version 2.0 (Frazer, Canham, & Lertzman, 1999), calculating the percentage of pixels that were open sky.

Thermal Preference

We measured the preferred temperature range, the central 50% of body temperatures, measured from lizards allowed to choose body temperatures in a thermal gradient free of other environmental constraints (Hertz et al., 1993), for male lizards caught in urban and natural sites

221   (*A. cristatellus*: natural $N = 24$, urban $N = 21$; *A. sagrei*: natural $N = 14$, urban $N = 15$). Lizards

222   were housed at the University of Rhode Island under a 12L:12D cycle for five to 42 days after

223   capture, fed crickets every three days (except 24 hrs before a trial) and misted three times per

224   day. We measured thermal preferences by placing individuals in a thermal gradient comprised of

225   eight visually and physically separated lanes, to run multiple lizards simultaneously. We placed

226   an incandescent heat lamp at one end of the lane for basking at high temperatures, while

227   underneath the opposite end of the gradient we placed a small plastic container filled with ice.

228   The average temperature at the warm end of the gradient was 46.6 °C (SE=0.30; range=44-52°C)

229   and 15.4 °C (SE=0.28; range=7-17°C) at the cold end. For both species, temperatures in all

230   gradients always included the range of preferred temperatures and temperatures up to critical

231   thermal maxima previously reported in the literature (Corn, 1971; Hertz et al., 1993). We

232   measured internal body temperatures of lizards using a thermocouple (K-type, 36-guage, 0.13

233   mm-diameter) inserted in the cloaca and taped to the body, leaving lizards free to move

234   throughout the thermal gradient. We recorded body temperatures every ten seconds, allowing

235   continuous monitoring of body temperature without disturbance by observers. After acclimating

236   to the lanes for 30 minutes, lizards were allowed to select body temperatures for between three

237   and four hours. We excluded lizards from the experiment if thermocouples became detached or

238   lizards showed abnormal behavior. In these cases, lizards were given one additional trial, but

239   were completely excluded from analyses if they never performed.

240   **Thermoregulatory Effectiveness**

241   To determine how accurately a lizard achieves a preferred body temperature, given the

242   available thermal habitat, we calculated thermoregulatory effectiveness (*E*) for adult lizards

243   observed in the wild with the following equations: $E = 1 - d_b/d_e$, where d_b and d_e refer to the

244   mean deviation of T_b and T_e from the preferred temperature range, respectively (Hertz et al.,

245   1993). Values of E approaching one signify a highly-effective thermoregulator, whereas values

246   of E approaching zero represent a thermoconformer or an organism behaviorally passive in terms

247   of temperature regulation. A negative E indicates avoidance of preferred thermal habitat. We set

248   confidence intervals on E values through 1000 replicates of bootstrap resampling of our field

249   measurements of T_e and T_b for each site. We computed d_b and d_e by randomly drawing samples

250   (with replacement) of n observations (total number of observations) of T_e and T_b. We also

251   calculated the percentages of models and lizards below, within, and above their T_{pref} range.

252   **Thermal Performance**

253   We generated thermal performance curves by recording maximum sprint velocity on a

254   standard racetrack, a 8.6 cm-wide board covered in window screen at a 37° angle to encourage

255   quadrupedal movement, at five temperatures (15°C, 20°C, 25°C, 30°C, and 35°C) for *A.*

256   *cristatellus* and six temperatures (15°C, 20°C, 25°C, 30°C, 35°C, and 40°C) for *A. sagrei*. We

257   collected males of both *A. cristatellus* and *A. sagrei* from urban sites, Red (N = 15) and Gables

258   (N = 15), respectively, and natural sites, Matheson (N = 13) and Montgomery (N = 15),

259   respectively. These were a different set of lizards than those used for the thermal preference

260   experiment and were held under the same conditions. We kept lizards in an incubator for at least

261   30 minutes to reach the target temperature. Lizards were placed at the base of each track and

262   allowed to run upwards. We encouraged movement with gentle taps near their tails when needed.

263   We filmed all lizard runs at 240 frames-per-second with a digital camera (Casio Exilim Ex-

264   zr1000), and used ImageJ (Schneider, Rasband, & Eliceiri, 2012) to determine maximum

265   velocity. For *A. sagrei* thermal performance curves, we anchored the high end of the TPCs with

266   mean critical thermal maximum (CT_{max}) temperatures, calculated as the temperature at which

267 righting response is lost, from a different data set for nearby urban (41.1 °C) and natural (40.6

268 °C) locations in Miami (Battles, unpublished data). For *A cristatellus*, we added CT_{max} values for

269 urban and natural *A. cristatellus* populations in Miami, which did not differ from each other

270 (39.0°C; Leal & Gunderson 2012). To estimate thermal performance curves, following Logan et

271 al. (2014), we fitted data with 21 asymmetrical peak curves using TableCurve 2D (SysStat

272 Software Inc, San Jose, CA). For each individual, we calculated AIC scores of the generated

273 models and chose the best fit. When AIC values were too close to identify a single model, we

274 chose the model with fewer parameters, and when models with the fewest parameters were

275 indistinguishable, we chose the model with the highest R^2 value.

276 **Statistics**

277   We performed all statistical analyses in R (R Core Team, 2015), and analyzed species

278 separately, except when specified otherwise. We performed an ANOVA of available canopy

279 openness by site nested within site type (natural or urban), followed by Tukey-HSD post-hoc

280 analysis to determine differences among sites. To test whether the two species use different

281 microhabitats from that available and from each other when they co-occur at the same urban sites

282 (i.e., Crandon and Red), we compared the availability of canopy openness to locations used by

283 lizards using ANOVA and Tukey-HSD post-hoc tests. In urban sites with only *A. sagrei* (i.e.,

284 Gables and UM), we compared canopy openness availability and use with a t-test. Natural sites

285 lacked variation in canopy cover, so we did not test for differences between availability and use

286 by lizards. To measure the effect of canopy openness on T_e, we performed a mixed-model

287 ANCOVA with site, model ID, and time of day as random effects. Then, for only the urban sites

288 where canopy openness had an effect on temperature, we performed a mixed-model ANCOVA

289 of T_e by canopy openness with site and model ID as random effects, for each hour of the day.

290   To analyze thermal availability, we performed a mixed-model ANOVA testing for

291   differences in T_e by site type with time of day and model ID as random effects. To test for

292   differences between T_b and T_e, we performed a mixed-model ANOVA of temperature by type

293   [T_e (copper model) or T_b (*A. cristatellus*, and *A. sagrei*)] and site, and their interaction, with ID

294   (lizards and model) and time of day as random effects. We used post-hoc Tukey-HSD tests to

295   test for differences between models and lizards in each site.

296   Following estimation of thermal performance curves (see above), we used t-tests to

297   compare moments on TPC: optimal performance temperature (T_{opt}), maximal sprint speed (P_{max}),

298   and performance breadth (95% T_{Br} and 80% T_{Br}). The performance breadth is the range of

299   temperatures at which sprint performance is at 95% and 80% of the maximal sprint speed,

300   respectively. Next, we used chi-square tests to compare portions of the TPC (95% T_{Br}, and 80%

301   T_{Br}) available and used in urban versus natural sites.

302   **RESULTS**

303   **Canopy Openness**

304   Urban areas had more open canopies than natural areas based on random model locations

305   ($F_{1, 251} = 256.5$, $P < 0.001$; Fig. 1), with significant variation among urban sites, but not natural

306   ones (Fig. 1; $F_{6, 251} = 10.0$, $P < 0.001$). Canopy openness strongly influenced T_e variation within

307   urban areas ($F_{1,1276} = 349.6$, $P < 0.001$), overall explaining 13.6% of temperature variation not

308   accounted for by variation between the sites, the time of day, and the model locations. The

309   strength of the effect of canopy openness on temperature in urban areas changed throughout the

310   day, with the strongest effects from late morning until mid-afternoon (Table 1). Because natural

311   areas had more closed canopies and less variation in canopy cover, we did not find a canopy

312   cover-temperature relationship in natural sites. In the urban sites with both species (i.e., Crandon

14

313 and Red), *A. cristatellus* used locations with significantly more closed canopies than both *A.*

314 *sagrei* and those available at random (Crandon: $F_{2, 276} = 24.4$, $P < 0.001$; Red: $F_{2, 294} = 18.3$, $P <$

315 0.001; Fig. 2). In the urban site Gables, which had the most open canopy of all sites, *A. sagrei*

316 used significantly more closed canopy locations than randomly available ($t = 2.6$, $df = 47.2$, $P <$

317 0.05; Fig. 2).

Field Operative and Body Temperatures

319 Operative temperatures (T_e) in urban areas were 1.5 °C warmer on average than in natural

320 areas ($F_{1, 264.7} = 120.3$, $P < 0.001$; Fig. 3). *Anolis cristatellus* T_b were on average 0.9 °C higher in

321 urban as compared to natural areas ($F_{1, 529} = 20.4$, $P < 0.001$), however, lizard T_b at the Bear

322 natural site did not differ from the urban sites. *Anolis sagrei* T_b were on average 2.5 °C higher in

323 urban compared to natural sites ($F_{1,793} = 181.0$, $P < 0.001$; Fig. 3). The only pair of urban sites in

324 which *A. sagrei* T_b differed significantly was Gables and Crandon ($t = 3.2$, $df = 793$, $P < 0.05$),

325 with lizard T_b at Gables being 1.0 °C higher.

Thermal Preference

327 The preferred temperature range (middle 50% of temperatures from the laboratory

328 gradient) for *A. cristatellus* was between 28.2°C and 31.7°C, and the preferred temperature range

329 for *A. sagrei* was between 30.2°C and 35.7°C. Neither species differed in thermal preference

330 between natural and urban populations. These preferences are consistent with previously

331 reported preferred temperature ranges of *A. cristatellus* (Hertz et al., 1993; Huey & Webster,

332 1976) and *A. sagrei* (Corn, 1971).

Thermoregulatory Effectiveness

Overall, lizard body temperatures (T_b) exceed T_e for both species ($F_{2,1722} = 186.8$, $P <$ 0.001; Figs. 3, 4, 5). For each species at each site, T_b were significantly higher than T_e, except for *A. sagrei* at Gables (Figs. 3, 4, 5; Tables 2, 3).

For both species, in urban and natural areas, body temperatures were closer to the preferred temperature range than were operative temperatures ($d_b < d_e$), with exception of *A. cristatellus* at Bear, suggesting that lizards actively thermoregulate at most sites (Tables 2, 3). *Anolis cristatellus* at urban and natural sites differ little in their thermoregulatory effectiveness (*E*), in contrast, *A. sagrei* appears to thermoregulate more effectively in urban areas than natural areas (Tables 2, 3). The negative *E* value for *A. cristatellus* in the Bear natural site suggests that these lizards avoid available microhabitats within the preferred temperature range (Table 2). Furthermore, *A. sagrei* generally thermoregulates more effectively than *A. cristatellus*, which means that *A. sagrei* maintains T_b within T_{pref} despite T_e being further outside the T_{pref} range of this species.

For *A. cristatellus*, the Matheson natural site had a higher percentage of models below the preferred temperature range than the other sites, and no models were above it (Fig. 6a). As shown by the *E* values, *A. cristatellus* in natural and urban sites have similar percentages of lizards within their preferred temperature range (Fig. 6, Table 2). Compared to *A. sagrei*, *A. cristatellus* at urban sites and the natural site Bear have higher percentages of lizard T_b above the preferred temperature range (Figs. 6b-d, 7).

For *A. sagrei*, urban sites Crandon and Red were similar to natural sites in that they had a high percentage of T_e below the preferred temperature range (Fig. 7a-d). Despite having similar T_e profiles as natural sites, lizards in the Crandon and Red urban sites are most often found

356 within their preferred temperature range (Fig. 7c, d). In contrast, the more urbanized sites of

357 Gables and UM had low percentages of T_e (and T_b) below the preferred range (Fig. 7e, f). The

358 percentage of lizard T_b within their preferred range was similar across all urban sites (Fig. 7c-f).

Occupancy Limitations

360 Both species co-occur at urban sites Red and Crandon. Where the species occur alone, a

361 greater portion of T_e values are within their preferred range compared to the preferred range of

362 the other species, except for the natural sites where *A. sagrei* are found (Tables 4). At the time of

363 this study, these natural sites (Barnes and Montgomery) were outside the distribution of *A.*

364 *cristatellus* in Miami.

Thermal Performance

366 Optimal performance temperature, maximal sprint speed, and thermal performance

367 breadth did not differ between urban and natural lizards for either species. However, compared to

368 *A. cristatellus*, *A. sagrei* had a higher optimal performance temperature (T_{opt}; 37.99 °C vs. 33.96

369 °C) and greater maximal sprint speed (1.74 ms^{-1} vs. 1.40 ms^{-1}). Furthermore, the temperatures at

370 which *A. sagrei* could achieve 95% and 80% of T_{opt} (performance breadth: T_{br}) were higher than

371 those for *A. cristatellus* (95% T_{br} *A. cristatellus*: 30.85 °C – 34.95 °C, *A. sagrei*: 34.38 °C –

372 38.37 °C; 80% T_{br} *A. cristatellus*: 25.66 °C – 35.58 °C, *A. sagrei*: 29.70 °C – 39.22 °C). See S5

373 in the supporting information for a TPC figure and table for TPC values.

374 For both species, compared to natural areas, operative temperatures in urban areas

375 provide more access to the temperatures at which lizards can achieve 95% optimal performance

376 (*A. cristatellus*: X^2= 39.1, df= 1, $p < 0.001$; *A. sagrei:* X^2= 105.3, df= 1, $p < 0.001$) (Table 6).

377 Operative temperatures in urban areas provide more access to the temperatures at which lizards

378 can achieve 80% optimal performance for *A. sagrei* (X^2= 100.3, df= 1, $p < 0.001$), but urban and

379 natural sites were equal for *A. cristatellus*.

380   Lizards were found at body temperatures conferring 80% and 95% of optimal

381 performance more often in urban areas than in natural areas (80% T_{br} *A. cristatellus*: X^2= 5.1, df=

382 1, $p < 0.05$; 80% T_{br} *A. sagrei:* X^2= 72.1, df= 1, $p < 0.001$; 95% T_{br} *A. cristatellus*: X^2= 32.2, df=

383 1, $p < 0.001$; 95% T_{br} *A. sagrei:* X^2= 55.1, df= 1, $p < 0.001$; Table 5).

384 **DISCUSSION**

385   Urbanization converts natural habitats into landscapes dominated by open space and

386 human-made structures, altering the thermal environment for small ectotherms. As predicted, we

387 found that canopies were over three times more open in urban areas (32%) than natural areas

388 (9%; Fig. 1), contributing to increased mean operative temperatures in urban habitats. These

389 findings support patterns of higher temperatures in urban areas, which are strongly influenced by

390 reduced tree cover (Georgi & Zafiriadis, 2006; Zhou, Huang, & Cadenasso, 2011). We further

391 demonstrated this relationship at a scale relevant to small ectotherms, highlighting the variation

392 in both canopy cover and thermal availability within urban areas. Not only were operative

393 temperatures higher in urban areas, but lizard body temperatures were also higher. Our study is

394 one of the first to demonstrate the consequences of urban heat islands for small ectotherms. Our

395 mechanistic perspective revealed that urban and natural areas represent distinct thermal

396 microhabitats in which ectotherms may experience shifts in thermoregulatory costs and changes

397 in the constraints on temperature-dependent activity and performance, which should ultimately

398 influence their ability to persist these habitats.

399   How increased temperatures in urban areas influence thermoregulatory costs for small

400 ectotherms and thus the thermal suitability of urban habitats will vary both by a species'

401 physiological traits and the availability of thermal microhabitat. Even though urban areas

402 increase the availability of warm, sunny patches, for some species they could be distributed such

403 that an urban area is too open, without enough nearby shade, increasing thermoregulatory costs

404 for that species (Angilletta, 2009; Huey, 1974; Huey & Slatkin, 1976). However, in our sites,

405 lower d_e values in urban sites (with exception in Bear natural site, discussed below), indicate

406 reduced mean deviation of operative temperatures from the preferred temperature range for the

407 species present. In this sense, energetic costs of moving to warm patches will be lower when the

408 frequency of sunny patches is increased (Gunderson & Leal, 2012). Thermoregulation is also

409 used to decrease body temperature, and therefore ectotherms incur costs when operative

410 temperatures exceed thermal preferences (common in our study) or tolerances (rare in our study).

411 In these cases, such as for *A. sagrei* at the Gables urban site where lizards used locations with

412 more canopy cover than randomly available, thermoregulatory costs may increase in urban areas,

413 as lizards seek out scarce or widely separated cool, shaded spots to reduce T_b (Vickers,

414 Manicom, & Schwarzkopf, 2011). In addition to the presence of sunny and shady microhabitats,

415 their spatial distribution also determines thermoregulatory costs (Sears & Angilletta, 2015). Our

416 study prioritized comparing operative and body temperatures for urban and natural sites, rather

417 than their arrangement within sites, but future studies could evaluate how the spatial distribution

418 of sunny and shady patches in urban areas influences thermoregulatory costs. We expect that

419 buildings have a strong impact on thermoregulatory costs related to moving between patches,

420 such that a single side of a building can be entirely shaded for several hours, while just a short

421 distance away, perhaps around a corner, lizards could access full sun or a mixture of sunny and

422 shady locations. Thermoregulatory costs are important to consider because they determine the

423 ease with which ectotherms can achieve optimal temperatures for performance and maintain

424 preferred temperatures, which should ultimately influence fitness (Gunderson & Leal, 2015;

425 Huey & Berrigan, 2001).

426 For *A. sagrei*, urban areas increase access to preferred body temperatures, which should

427 result in higher rates of activity. Temperature is one of the most important drivers of ectotherm

428 activity (e.g. foraging, territory defense, and mating) and occurs at its highest levels when

429 organisms are within their range of preferred body temperatures (Grant & Dunham, 1988;

430 Gunderson & Leal, 2016). Despite increased mean temperatures in urban areas, urban

431 populations of our study species did not have warm-shifted thermal performance curves or

432 higher thermal preferences. Because *A. sagrei* can spend more time within T_{pref} in urban sites,

433 this species may benefit from the thermal microhabitats of urban areas, likely reproducing at

434 higher rates than in natural habitat (Huey & Berrigan, 2001). For example, in more open, warmer

435 habitat compared to cooler, close-canopied forest, female *A. cristatellus* in Puerto Rico were

436 more likely to be reproductive year-round, likely due to increased basking opportunities to

437 achieve higher body temperatures (Otero, Huey, & Gorman, 2015). Furthermore, higher *E* values

438 for *A. sagrei* in urban sites indicate that even when operative temperatures deviate far from

439 preferred temperatures, lizards still precisely thermoregulate to maintain body temperatures

440 within the preferred range (Hertz et al., 1993). Therefore, urban habitats are more favorable for

441 *A. sagrei*, which may have trouble persisting in more close-canopied sites, such as forested

442 habitats, that restrict their ability to achieve higher body temperatures. It is important to note that

443 while costs of thermoregulation may be lower in urban sites, Basson et al. (2017) showed that

444 even in a low-quality thermal habitat with high thermoregulatory costs in the lab, *Cordylus*

445 lizards prioritized maintaining T_b within T_{pref}. It may be necessary to maintain warmer body

446 temperatures that confer higher activity in urban habitats in the Miami area, even if costly, to

447   successfully compete with multiple other introduced and native anoles (Kolbe et al., 2007), or

448   manage urban predation pressure (Chejanovski, Avilés-Rodríguez, Lapiedra, Preisser, & Kolbe,

449   2017).

450   In contrast to *A. sagrei*, *A. cristatellus* may not find urban sites more favorable than

451   natural habitat. The thermoregulatory effectiveness (*E*) for *Anolis cristatellus* was not

452   significantly different between urban and natural sites (Table 2). These values are similar to

453   estimates for *A. cristatellus* in xeric habitats (warm and dry) in their native range, where lizards

454   actively thermoregulate (Gunderson & Leal, 2012). However, thermoregulatory effectiveness

455   was negative in the Bear natural site. Negative *E* values suggest lizards are avoiding or restricted

456   from using sites with preferred temperatures, perhaps due to predation pressure or competitors

457   (Hertz et al., 1993), but unfortunately we could not identify any obvious factors causing this at

458   the Bear site. In urban areas, operative and body temperatures for *A. cristatellus* were less often

459   within preferred temperature range, which suggests that urban areas may constrain activity for

460   this species. Similarly, Kaiser et al. (2016) found that a more-thermophilic butterfly species had

461   increased survival and greater body size in urban areas than did a woodland species adapted for

462   cooler conditions. Furthermore, if operative temperatures too frequently exceed thermal

463   tolerances, or if the habitat lacks enough cool refuges, certain ectotherms could be excluded from

464   urban areas altogether (Chown & Duffy, 2015). Interestingly, Hall and Warner (2017) found that

465   female *A. cristatellus* from one of our urban sites, Red, had greater body condition and fecundity

466   than lizards from one of our natural sites, Matheson. Our findings on operative and body

467   temperatures suggest that factors other than temperature likely contribute to body condition and

468   fecundity increases. Certainly, animals in urban areas have been found to express a longer

469   reproductive period than in their natural habitat, but other determinants, such as food availability,

470   may be important as well (Lowry, Lill, & Wong, 2013). However, Hall and Warner (2017) found

471   that fecundity increased in urban areas because females began laying eggs earlier in their lab

472   setting. We conducted our study in the summer, but urban areas may be more favorable to *A.*

473   *cristatellus* during other seasons if urban areas reach preferred temperatures more often than

474   natural areas, such as earlier in the spring when reproductive activity is beginning (Gorman &

475   Licht, 1974; Hall & Warner, 2017; Lee, Clayton, Eisenstein, & Perez, 1989). The different

476   responses to urban habitats of the lizard species in our study show that warmer urban habitats

477   will not benefit all ectotherms equally.

478   Beyond the thermal suitability for a single species, competition on thermal niche axes can

479   further limit persistence. For instance, in the Matheson natural site, which had the lowest mean

480   operative temperatures, 40% of operative temperatures are within the preferred range of *A.*

481   *cristatellus*, whereas only 3% would be within the preferred range of *A. sagrei* (Table 4).

482   Similarly, in Puerto Rico, *A. cristatellus* and *A. gundlachi* both occupy forest habitats, but only

483   *A. gundlachi* is found above ~300 m elevation (Gorman & Hillman, 1977). The mean available

484   temperature in the forest above 300 m is at the low threshold for activity of *A. cristatellus*, but in

485   the middle of activity range for *A. gundlachi* (Gunderson & Leal, 2016; Gorman & Hillman,

486   1977). Both species in our study co-occur along the edges of the Matheson forest patch, which is

487   < 1 km away from our urban site Red, but *A. sagrei* was never found in the forest at Matheson.

488   With conditions in almost the entire forest below its T_{pref}, *A. sagrei* cannot reach activity levels

489   to forage, mate and defend territories effectively. This likely puts *A. sagrei* at a competitive

490   disadvantage, and it may be excluded from large, forested areas with *A. cristatellus* in Miami.

491   Similarly, at the Gables urban site, 62% of T_e are within the preferred range of *A. sagrei*, but

492   only 26% are within the preferred range of *A. cristatellus* (Table 4). With greater potential for

493   higher activity rates, *A. sagrei* has a substantial competitive advantage. Yet, not all types of

494   urban habitat exclude *A. cristatellus*. In the sites with both species (i.e., Crandon and Red), *A.*

495   *sagrei*, which preferred warmer temperatures, selected microhabitats with more open canopies

496   and achieved higher T_b than did *A. cristatellus* (Fig. 2). These sites differed from the two urban

497   sites with only *A. sagrei* in that the operative temperature distributions encompassed the T_{pref}

498   ranges of both species. While competition between these two species could influence divergence

499   in thermal traits, T_{pref} ranges did not differ between allopatry and sympatry in either species. Yet,

500   divergence in T_{pref} allows them to partition the thermal niche, at least in some habitats

501   (Magnuson, Crowder, & Medvick, 1979; Paterson & Blouin-Demers, 2017). Interestingly, the

502   natural sites that *A. sagrei* occupies, Barnes and Montgomery, seem more favorable to *A.*

503   *cristatellus* than for *A. sagrei* (Table 4). If *A. cristatellus* is ever transported to these natural sites

504   or expands its distribution to include them, we predict that *A. sagrei* would be out-competed and

505   displaced by *A. cristatellus,* which is better suited thermally for these forested areas (Kolbe et al.

506   2016).

507   The success and spread of introduced species will rely upon suitable thermal

508   microhabitats for persistence. Abiotic factors, such as temperature, play an important role in

509   where invasive species can or cannot persist (Bomford, Kraus, Barry, & Lawrence, 2009; Ulrichs

510   & Hopper, 2008; Zenni & Nuñez, 2013). Because urbanization greatly increases species

511   introductions (Shochat et al., 2010), the concurrent temperature increases associated with urban

512   areas may enhance ectotherm invasion success for some species. In our case, numerous

513   populations of *A. sagrei* have been documented outside their native range, often associated with

514   human activity (Campbell, 1996; Godley, Lohrer, Layne, & Rossi, 1981; Kolbe, Ehrenberger,

515   Moniz, & Angilletta, 2014; Norval, Mao, Chu, & Chen, 2002), and the favorability of urban

516 thermal conditions for *A. sagrei* is likely a key factor in this species' invasion success (Angetter,

517 Lötters, & Rödder, 2011). Outside of anoles, warmer conditions and human habitat modification

518 improve the invasion success of the Argentine ant in many locations around the world (Roura-

519 Pascual et al., 2011). However, even ectotherms that benefit from warmer temperatures are still

520 limited by low temperatures due to seasonality or elevation (Angilletta, 2009; Sunday, Bates, &

521 Dulvy, 2012). Urban areas may increase mean daily temperatures overall, but the magnitude and

522 effect depends on the regional climate (Imhoff et al., 2010; Roth, Oke, & Emery, 1989). Yet,

523 anole species have been shown to decrease their low-temperature tolerance by acclimation

524 (Kolbe et al., 2012), and *A. sagrei* CT_{min} decreases with increasing latitude (Kolbe et al., 2014).

525 Flexibility in low temperature tolerance combined with increased activity time and reduced

526 thermoregulatory costs may make cities more favorable for invasive species like *A. sagrei*.

527   Alternatively, *A. cristatellus* represents an example of the opposite effect of urbanization

528 on invasion. In a study exploring the spread of *A. cristatellus* in Miami, Kolbe et al. (2016) found

529 that this species is positively associated with dense vegetation, high canopy cover, and forest

530 patches, thus limiting its dispersal through the fragmented city. Our study corroborates these

531 habitat requirements and explains a possible mechanism for why very warm urban sites, where

532 *A. sagrei* are common, may exclude *A. cristatellus*. Hourly temperature (T_e) for the urban site

533 Gables, for example, reveal that *A. cristatellus* could achieve preferred temperatures easily in the

534 early mornings and evenings (Fig. 4), but this would be difficult or impossible throughout the

535 mid-day because of the lack of canopy cover (Fig. 1). Therefore, high-temperature environments

536 without enough thermal heterogeneity, such as this more-open urban site, can limit activity time

537 and reduce persistence for species like *A. cristatellus* (Lara-Reséndiz, Gadsden, Rosen, Sinervo,

538 & Méndez-De la Cruz, 2015). Furthermore, if *A. cristatellus* were in Gables or similar urban

539 locations throughout Miami, it would have the additional stress of more often needing to avoid

540 its upper thermal tolerance (CT_{max}) compared to the urban sites where it is found (Crandon and

541 Red). If high temperatures limit persistence, then dispersal of introduced species with similar

542 thermal traits throughout urban areas will be restricted. Urbanization often exists as a gradient of

543 intensity (Luck & Wu, 2002; McDonnell & Pickett, 1990), and some levels of urban

544 development are suitable for introduced species while others are not (Crooks, Suarez, & Bolger,

545 2004; Grarock, Tidemann, Wood, & Lindenmayer, 2014). Research on the urban heat island

546 effect shows a similar thermal gradient of intensity because of urban development (Rizwan et al.,

547 2008), and variation in thermal quality may affect invasive ectotherms in a similar manner

548 (Chown & Duffy, 2015). Indeed, our natural sites are part of an urban matrix and our urban sites

549 are not entirely barren, suggesting our already significant results are conservative relative to

550 more extreme comparisons on the urban-natural gradient.

551   Temperature, and other abiotic factors, likely play a major role in the persistence and

552 spread of introduced ectotherms. Under the right thermal conditions, ectotherms can be more

553 competitive and reproduce at greater rates than other species (Huey & Berrigan, 2001; Otero et

554 al., 2015). In this study, we show that urbanization significantly alters thermal habitats for

555 ectotherms, increasing both ambient temperature and the availability of warm microhabitats.

556 Urban thermal habitat may confer decreased costs of thermoregulation for ectotherms, but urban

557 areas in Miami impact the persistence and spread of two introduced species in opposing ways.

558 With reduced thermoregulatory costs and increased time spent within T_{pref}, *A. sagrei* likely finds

559 urban areas thermally superior to natural habitat in Miami. In contrast, because *A. cristatellus* T_b

560 are within T_{pref} less often in urban habitats and *A. cristatellus* is at a disadvantage competing with

561 *A. sagrei* from a thermal perspective, they are likely excluded from much of urbanized Miami, an

562 effect that increases with urbanization. Many other factors, such as competition, predation, prey

563 abundance, and disease, could influence persistence in urban areas. However, the thermal quality

564 of urban habitats is certainly a fundamental aspect of urban environments for ectotherms. Our

565 study provides a foundation for studying how the thermal characteristics of urban habitats

566 influence ectothermic organisms. Future studies should consider these findings when evaluating

567 and predicting the spread of introduced species.

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844

TABLES

846	Table 1 For each hour of lizard activity, effect of canopy openness on T_e in urban areas, degrees

847	of freedom in the denominator (df of numerator $= 1$), the coefficient estimate, and the percent of

848	variance explained by the canopy openness, without the random effects (marginal R^2).

Hour	F	Denominator df	Coefficient estimate	Variance explained (marginal R^2)
0700	1.76	112.7	0.00	0.01
0800	23.49**	114.0	0.06	0.16
0900	46.65**	113.9	0.10	0.28
1000	82.70**	114.0	0.11	0.41
1100	63.37**	113.6	0.10	0.32
1200	60.01**	112.9	0.10	0.29
1300	43.18**	112.1	0.07	0.18
1400	50.38**	115.6	0.07	0.23
1500	57.68**	66.5	0.05	0.33
1600	37.90**	115.9	0.04	0.20
1700	9.45*	114.9	0.03	0.04

849	$**P < 0.001, *P < 0.01$

850

851   Table 2 Summary statistics showing behavioral thermoregulation for *A. cristatellus* in two

852   natural (N) and two urban sites (U).

Site	t-value	d_b	d_e	d_e- d_b	E (95% CI)
Matheson (N)	**5.57**	1.18	1.68	0.50	0.296 (0.290 - 0.302)
Bear (N)	**4.70**	0.45	0.33	-0.12	-0.369 (-0.382 - -0.356)
Crandon (U)	**4.10**	0.54	0.99	0.45	0.454 (0.450 - 0.458)
Red (U)	**6.10**	0.77	1.11	0.34	0.304 (0.299 - 0.309)

853   *t*-statistic = post-hoc comparison from T_b vs T_e model (significant values, $P < 0.05$, in bold), d_b =

854   mean absolute deviation of T_b from preferred temperature range, d_e = mean absolute deviation of

855   T_e from the preferred temperature range, E = effectiveness of behavioral thermoregulation (Hertz

856   et al., 1993) and 95% confidence interval.

857

858   Table 3 Summary statistics showing behavioral thermoregulation for *A. sagrei* in two natural (N)

859   and four urban (U) sites.

Site	t-statistic	d_b	d_e	d_e- d_b	E (95% CI)
Barnes (N)	**6.64**	0.84	1.37	0.53	0.391 (0.386 - 0.397)
Montgomery (N)	**6.40**	1.00	2.45	1.45	0.587 (0.584 - 0.589)
Crandon (U)	**12.26**	0.49	1.96	1.47	0.750 (0.747 - 0.753)
Red (U)	**11.68**	0.48	1.65	1.17	0.711 (0.706 - 0.715)
Gables (U)	1.36	0.31	0.94	0.63	0.667 (0.663 - 0.672)
UM (U)	**6.13**	0.24	0.61	0.37	0.588 (0.582 - 0.594)

860   *t*-statistic = post-hoc comparison from T_b vs T_e model (significant values, $P < 0.05$, in bold), d_b -

861   = mean absolute deviation of T_b from preferred temperature range, d_e = mean absolute deviation

862   of T_e from the preferred temperature range, E = effectiveness of behavioral thermoregulation

863   (Hertz et al., 1993) and 95% confidence interval.

864

865   Table 4. The percentage of time that operative temperatures (T_e) are within the preferred

866   temperature range (T_{pref}) for the species that is present at a site (i.e., *A. cristatellus* at Matheson

867   and Bear, and *A. sagrei* at Barnes, Montgomery, Gables, and UM), and the predicted values for

868   the absent species if it were to occur there. Sites where the absent species is predicted to find the

869   thermal conditions more suitable than the species currently occupying that site are in bold.

Site	Percentage of time T_e is within T_{pref}	
	Actual % for Species Present	Predicted % for Species Absent
	A. cristatellus	*A. sagrei*
Matheson	40.1%	3.1%
Bear	68.8%	34.1%
	A. sagrei	*A. cristatellus*
Barnes	**36.7%**	**65.9%**
Montgomery	**14.5%**	**28.7%**
Gables	62.4%	26.1%
UM	68.1%	38.7%

870

871

872   Table 5 Percentage of time operative and body temperatures are within the 95% and 80%

873   performance ranges estimated from the thermal performance curves of lizards from natural and

874   urban areas.

Site Type	Operative Temperature		Body Temperature	
A. cristatellus	95% T_{Br}	80% T_{Br}	95% T_{Br}	80% T_{Br}
Natural	13.5%	76.2%	39.0%	90.2%
Urban	22.3%	75.6%	63.9%	95.5%
A. sagrei				
Natural	0.3%	31.0%	4.2%	60.2%
Urban	8.9%	48.0%	26.4%	86.9%

875   95% T_{Br} = range of temperatures that confer 95% P_{max}; 80% T_{Br} = range of temperatures that

876   confer 80% P_{max}.

877

878   **FIGURES**
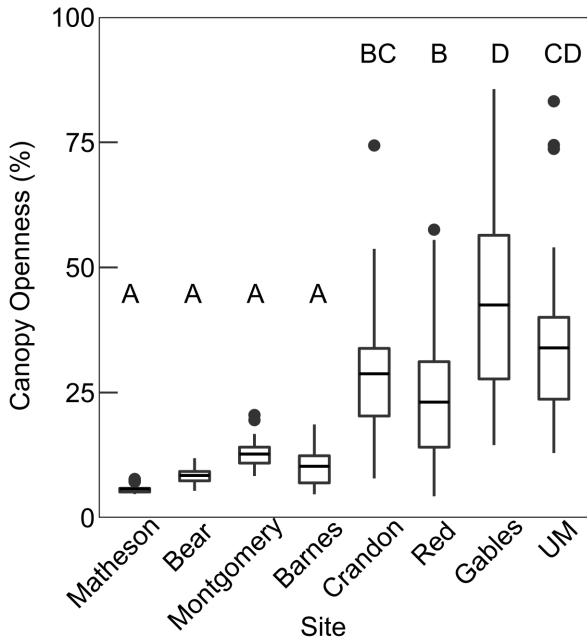
879

880   Figure 1 Mean percentage canopy openness (horizontal line) at random model locations, middle

881   50% of values (box), values within 1.5 times the interquartile range (whiskers), and outlying

882   values (points) for each site. Different letters denote statistically significance differences (P <

883   0.05) in mean values among sites based on Tukey-HSD post hoc tests.

884
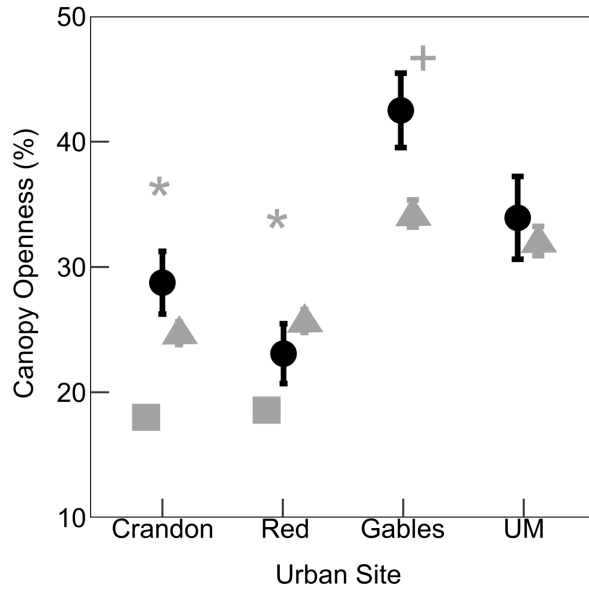
885

886 Figure 2 Mean canopy openness (± S.E.) of model locations (random availability; black) and

887 microhabitats used by *A. cristatellus* (grey squares) and *A. sagrei* (grey triangles) for the urban

888 sites. Asterisks indicate that *A. cristatellus* uses significantly shadier microhabitats than those

889 randomly available. The plus sign indicates that *A. sagrei* uses significantly shadier

890 microhabitats than those randomly available. Error bars are not visible in some cases when

891 smaller than the symbol for the mean value. Natural sites are not included because the variation

892 in canopy cover was too low for meaningful interpretation.

893

894
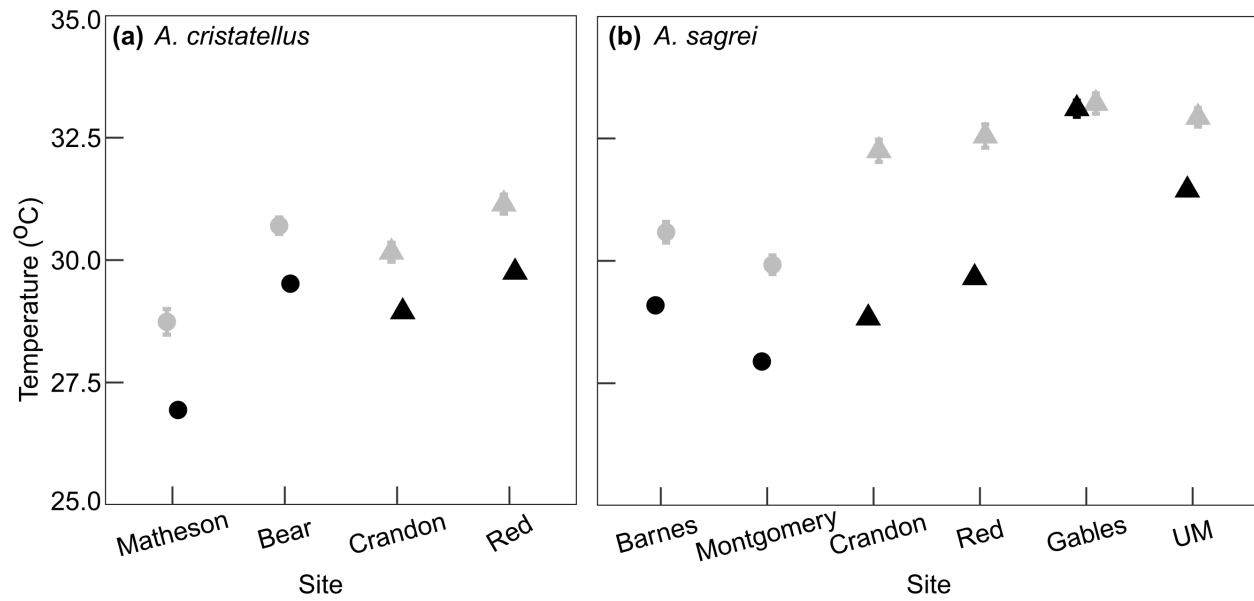
Figure 3 Mean (± S.E.) operative (black) and lizard body (grey) temperatures in natural (circles)

and urban (triangles) sites for A) *A. cristatellus* and B) *A. sagrei*. Data points are mean

temperatures for lizards captured during all times of the day sampled (0700–1800). Error bars are

not visible in some cases when smaller than symbols for mean values.

899

900
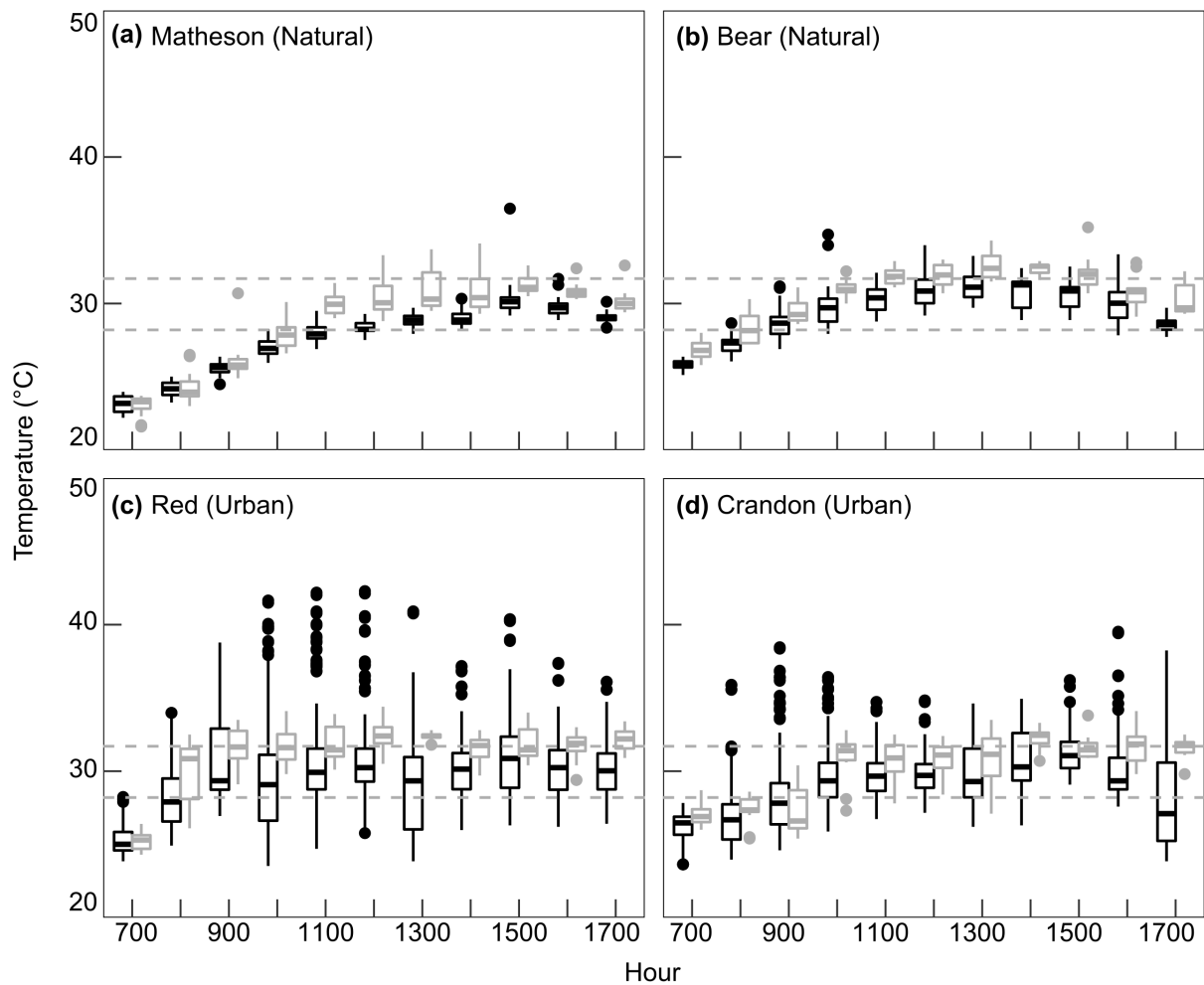
Figure 4 Boxplots showing operative temperatures (black) and lizard body temperatures for *A. cristatellus* (grey) throughout the day at each site with *A. cristatellus* present. Area between the dashed lines denotes the preferred temperature range as measured by a thermal gradient in the lab. For each hour of the day sampled, box plots show the median value (line within box), middle 50% of data (box), and values within 1.5 times the interquartile range (whiskers), with individual points as outlying data. See S4 in the online supporting information for panels of Red and Crandon (here, c & d) that also include *A. sagrei* body temperatures.

910
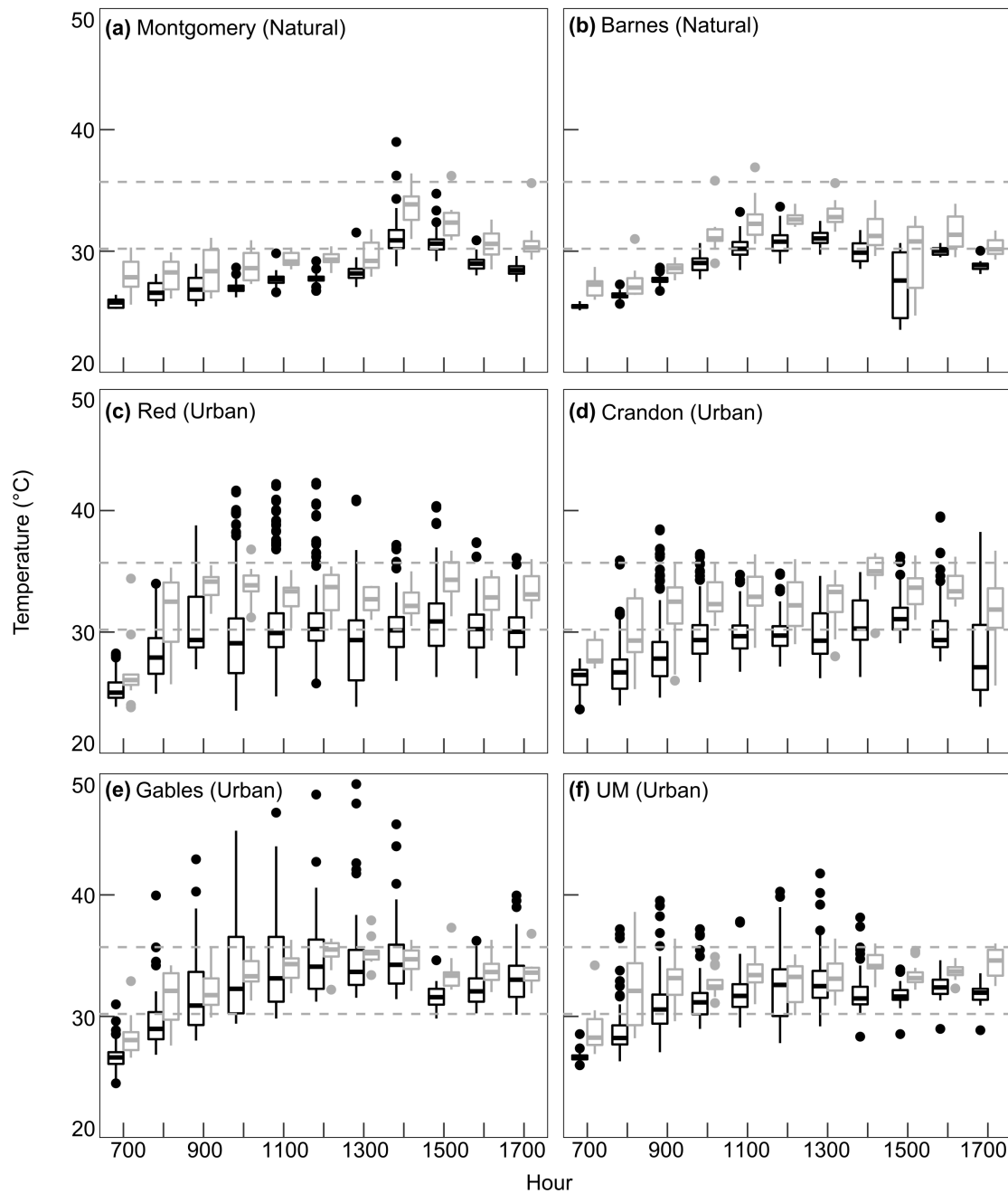
Figure 5 Boxplots showing operative temperatures (black) and lizard body temperatures for *A.*

sagrei (grey) throughout the day at each site with *A. sagrei* present. Area between the dashed

lines denotes the preferred temperature range as measured by a thermal gradient in the lab. For

each hour of the day sampled, box plots show the median value (line within box), middle 50% of

915   data (box), and values within 1.5 times the interquartile range (whiskers), with individual points

916   as outlying data. See S4 in the online supporting information for panels of Red and Crandon

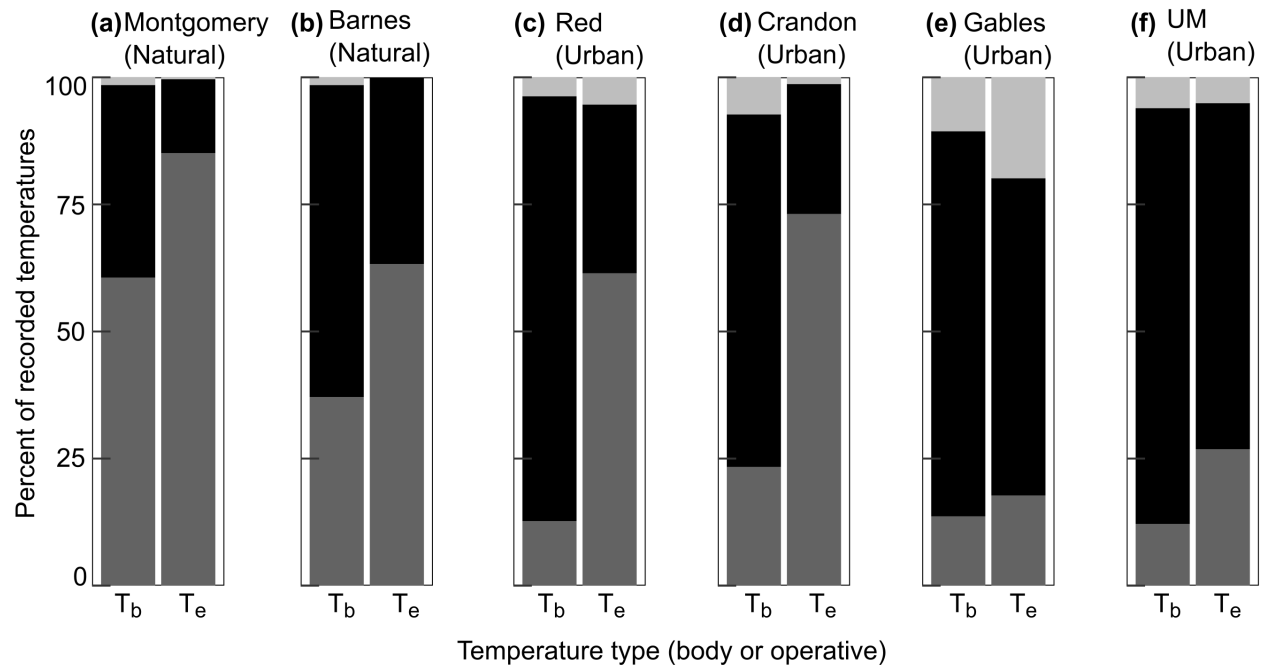917   (here, c & d) that also include *A. cristatellus* body temperatures.

918
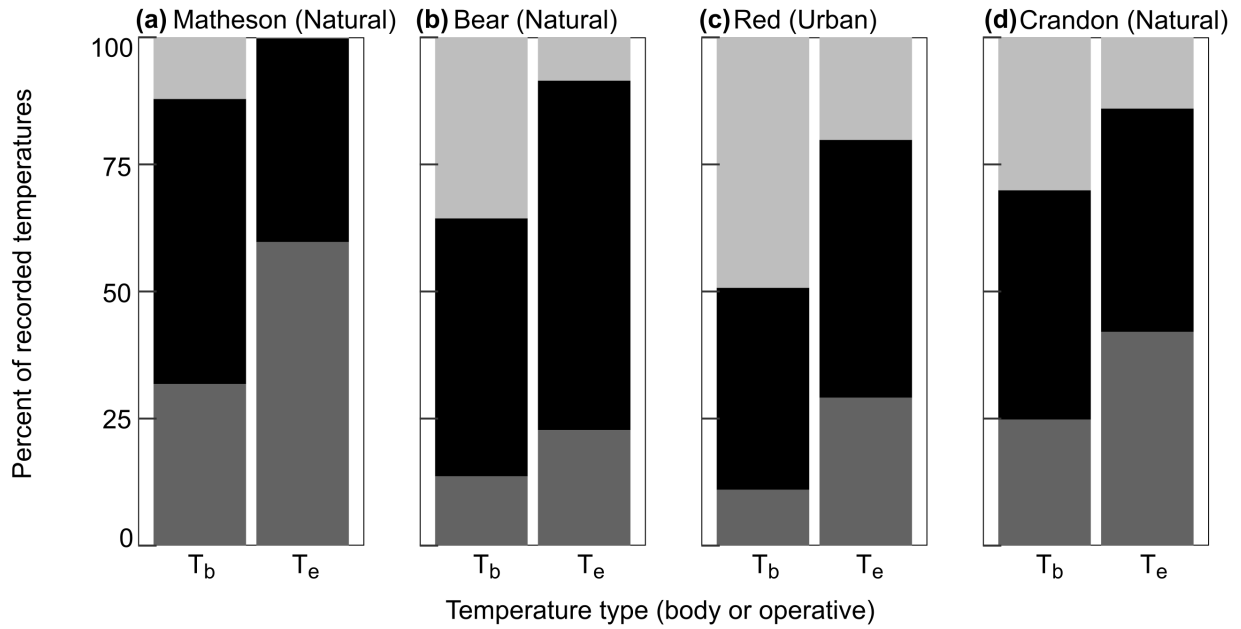
Figure 6 Percentage of body and operative temperatures below (dark grey), within (black), and above (light grey) the preferred temperature range (28.2°C – 31.7°C) for *A. cristatellus*. Each panel is a site where the species was present.

924

Figure 7 Percentage of body and operative temperatures below (dark grey), within (black), and

above (light grey) the preferred temperature range (30.2°C – 35.7°C) for *A. sagrei*. Each panel is

a site where the species was present

928