Oecologia

Temporal trade-off between territorial and thermoregulatory behaviors of a generalist lizard in a dry forest
--Manuscript Draft--

Manuscript Number:	OECO-D-23-00239
Full Title:	Temporal trade-off between territorial and thermoregulatory behaviors of a generalist lizard in a dry forest
Article Type:	Behavioral ecology –original research
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Suggested Reviewers:	M. Zachary Darnell, Dr. Associate Professor, University of Southern Mississippi zachary.darnell@usm.edu He has researched the trade-off between territorial and thermoregulatory behaviors with semi-aquatic animals in hot environments. Therefore, he has deep experience in this topic.
	Snow Bian, Dr. Adjunct Research Officer, La Trobe University S.Bian@latrobe.edu.au She has experience in assessing the effect of the environment, such as vegetation cover, on the effectiveness of mobile visual signals in animals such as push-ups.
	Jimena Bohórquez-Herrera, Dr. Full-time Professor, Universidad de Cartagena jbohorquezh1@unicartagena.edu.co She has researched the trade-off between territorial and thermoregulatory behaviors with semi-aquatic animals in hot environments, i.e., with elevated temperatures and intense solar radiation. Therefore, she has deep experience in this topic.
	Susan Cunningham, Dr. Senior lecturer, University of Cape Town susan.cunningham@uct.ac.za She has extensive knowledge about the opportunity and energetical costs of thermoregulatory behaviors in terrestrial animals in front of hot environments, even in terms of survival, growth, and reproduction.
	Kika Tuff, Dr. Founder of Impact Media Lab, Impact Media Lab kika@impactmedialab.com She has developed a framework for integrating thermal biology into fragmentation research that allow us to explore the physical and biological consequences of habitat loss in hot environments
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Funding Information:	Consejo Nacional de Ciencia y Tecnología (National Scholarship Program 2018–2022 (CVU: 664584)) MSc. Jose Israel Valencia-Esquivel
Abstract:	Avoiding dangerously hot body temperatures is important for survival, but animals may perform reproductive behaviors at the expense of behaviors used to cool down (or vice-versa), resulting in a thermoregulation-reproduction trade-off. Although this trade-off has been demonstrated in semi-aquatic animals, it has not been studied in terrestrial ectotherms. This is an important research gap given the importance of

survival-reproduction trade-offs in evolutionary ecology and the pace of habitat warming due to vegetation loss and global climate change. We explored this trade-off in territorial males of the lizard Sceloporus ochoterenae, which mates during the hot-dry season in seasonally dry tropical forest. We first confirmed the existence of a temporal trade-off between performing push-ups (a territorial behavioral display) versus sheltering in the shade (thermoregulatory behavior), then used confirmatory path analysis to explore how it is affected by vegetation cover, microclimate temperature, and the presence of a conspecific intruder. We found that territories with less vegetation cover had higher microclimate temperatures, where focal males spent more time performing push-ups at the expense of sheltering in the shade. Focal males also spent more time performing push-ups the longer an intruder was present, who was also affected by the environmental variables. Territorial males spent more time in sunny spots when performing push-ups despite the potential for overheating, perhaps because the display is more effective when performed in the open. The potential effects of continued habitat warming on this trade-off vary widely, including intensifying it, driving lizards to change their daily activity rhythms, and chronic overheating.

Cover Letter

CENTRO DE INVESTIGACIÓN EN BIODIVERSIDAD Y CONSERVACIÓN

UNIVERSIDAD AUTÓNOMA DEL
ESTADO DE MORELOS

CIβγC

Dr. Indrikis Krams
Editor-in-Chief
Oecologia

May 4, 2023

Dear Dr. Krams:

I am pleased to submit our manuscript entitled "Temporal trade-off between territorial and thermoregulatory behaviors of a generalist lizard in a dry forest" to be considered for publication as an "Original Research Article" in *Oecologia*.

We explored the temporal trade-off between territorial and thermoregulatory behaviors in terrestrial ectotherms by quantifying the time that territorial males of a generalist lizard species (*Sceloporus ochoterenae*) spent displaying push-ups (a territorial behavioral display) and sheltering in shady spots (a thermoregulatory behavior) in territories with different percentages of vegetation cover during the dry season of their mating season in a seasonally dry tropical forest. After confirming a negative relationship between these two behaviors, we used confirmatory path analysis to evaluate alternative hypotheses about the relationships among vegetation cover, microclimate temperature, the presence of territorial intruders, and male behavior. We found that focal males spent more time performing push-ups in more open territories, thus prioritizing territorial behaviors over thermoregulatory and antipredatory behaviors. Our results are similar to those of two recent studies in aquatic animals. To our knowledge, this is the first study of its kind in a terrestrial ectotherm, specifically in a habitat where the main thermal pressure is to cool down, rather than to warm up as in cool environments, which are very different scenarios. These results are especially relevant given the current rates of habitat warming due to deforestation and climate change, which are disproportionately affecting tropical ecosystems. We believe that these findings will be of interest to readers of *Oecologia*.

We declare that this manuscript is original, has not been published before, and is not currently being considered for publication elsewhere. As Corresponding Author, I confirm that all of the authors declare no conflicts of interest associated with this manuscript and that the manuscript has been read and approved for submission by all authors.

Thank you for your time.

Sincerely on behalf of all co-authors,

Israel Valencia Esquivel

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EM

Una universidad de excelencia

RECTORÍA
2017-2023

1   **Temporal trade-off between territorial and thermoregulatory behaviors of a generalist lizard**

2   **in a dry forest**

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10

14

15   **Abstract**

16   Avoiding dangerously hot body temperatures is important for survival, but animals may perform

17   reproductive behaviors at the expense of behaviors used to cool down (or vice-versa), resulting in a

18   thermoregulation-reproduction trade-off. Although this trade-off has been demonstrated in semi-

19   aquatic animals, it has not been studied in terrestrial ectotherms. This is an important research gap

20   given the importance of survival-reproduction trade-offs in evolutionary ecology and the pace of

21   habitat warming due to vegetation loss and global climate change. We explored this trade-off in

22   territorial males of the lizard *Sceloporus ochoterenae,* which mates during the hot-dry season in

23   seasonally dry tropical forest. We first confirmed the existence of a temporal trade-off between

24   performing push-ups (a territorial behavioral display) versus sheltering in the shade

25   (thermoregulatory behavior), then used confirmatory path analysis to explore how it is affected by

26   vegetation cover, microclimate temperature, and the presence of a conspecific intruder. We found

27   that territories with less vegetation cover had higher microclimate temperatures, where focal males

28   spent more time performing push-ups at the expense of sheltering in the shade. Focal males also

29   spent more time performing push-ups the longer an intruder was present, who was also affected by

30   the environmental variables. Territorial males spent more time in sunny spots when performing

31   push-ups despite the potential for overheating, perhaps because the display is more effective when

32   performed in the open. The potential effects of continued habitat warming on this trade-off vary

33   widely, including intensifying it, driving lizards to change their daily activity rhythms, and chronic

34   overheating.

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Introduction

Life history theory addresses the strategies used by organisms to allocate resources among self-maintenance, growth, and reproduction. These three components compete for a limited amount of energy, nutrients, and time, giving rise to trade-offs among them (Flatt & Heyland 2013). For example, resources invested in reproduction cannot be used for self-maintenance, leading to the trade-off between reproduction and self-maintenance (Stearns 1989). Investing more in reproduction than self-maintenance at a given time consumes energy reserves, decreases opportunities for other activities, and may jeopardize the individual's safety, which together may reduce the likelihood of their continued survival and/or ability to invest in potential future reproductive attempts, i.e., the trade-off between current and future reproduction (Flatt & Heyland 2013).

The trade-off between current and future reproduction has been explored considering longevity and fecundity in warm habitats. According to optimization models (Thunell et al. 2022) and experiments (Bestion et al. 2015), an increase in reproductive effort at the expense of a lower growth rate is favored in warm habitats, resulting in a demography characterized by smaller, younger adults with lower longevity but higher fertility (*the hotter is smaller* hypothesis, Kingsolver and Huey 2008). At the same time, growth rate trades off with longevity (Who-Seung et al. 2013). Reproductive effort generates reproductive costs, which in turn, can compromise survival so much as to truncate residual reproductive value prematurely. For example, reproductive behaviors during mating and gestation may increase the visibility of animals to their predators (Lorioux et al. 2013) or increase exposure to the lethal or sub-lethal effects of overheating (Darnell et al. 2020). Consequently, iteroparous animals may invest in behavioral adjustments that favor survival, such as antipredatory or thermoregulatory behaviors, while decreasing their investment in reproductive behaviors.

In sexually reproducing animals, finding and securing access to mates requires a series of behaviors that can incur energy, time, and safety costs. In many animals (e.g., *Austruca mjoeberg*, Darnell et al. 2020; *Pseudemoia entrecasteauxii*, Stapley 2006), territorial males attract attention

66   and communicate their quality to potential mates and conspecific intruders through territorial

67   behaviors such as static and mobile visual signals. Mobile visual signals cost energy (Zhu et al.

68   2020) and time (Allen and Levinton 2014); therefore, males should maximize the efficiency of their

69   signals (Fleishman & Font 2019), for example by displaying in sites that maximize their visibility.

70   Males of several lizard species tend to occupy and display in open, sunny spots during their

71   mating season (Martín and López 1999; Meek and Avery 2008; Carter et al. 2010). This may

72   increase the visibility of their mobile visual signals (Bian et al. 2019). However, open, sunny sites

73   also increase the risk of predation (Cooper & Vitt 2002), and in hot and dry ecosystems, sun

74   exposure increases the lethal and sub-lethal effects of overheating (i.e., that the individual's body

75   temperatures exceed its behavioral thermal tolerance range; Allen & Levinton 2014). Ectotherms

76   can avoid overheating by performing thermoregulatory behaviors, such as shuttling to cooler

77   microhabitats (Kearney 2013; Díaz et al. 2022). However, sheltering in shady microhabitats reduces

78   the opportunities to carry out activities in sunny microhabitats (e.g., behavioral displays; reviewed in

79   Cunningham et al. 2021). This is expected to result in a temporal trade-off between territorial and

80   thermoregulatory behaviors for males that tend to occupy and display in open, sunny spots during

81   their mating season in hot ecosystems. The existence of this trade-off has been demonstrated in

82   intertidal crabs (Darnell et al. 2020) and sea lions (Bohórquez-Herrera et al. 2014) during their

83   mating season, but not, to our knowledge, in any terrestrial vertebrate inhabiting hot, dry

84   environments.

85   The hot and dry conditions during the dry season in seasonally dry tropical forests (SDTF)

86   present a challenging context for thermoregulation and therefore offer an ideal context in which to

87   test the temporal trade-off between territorial and thermoregulatory behaviors. The SDTF has two

88   seasons marked by large differences in the amount of precipitation, with most trees losing their

89   leaves in the dry season to conserve water (Siliceo-Cantero et al. 2016). This seasonal defoliation

90   increases the amount of solar radiation that reaches the ground, increasing in turn both the

91   visibility (Ferreira & Faria 2021) and the ambient temperature of the habitat (Valenzuela-Ceballos

92   et al. 2015). In addition, the abundance of arthropods decreases during the dry season (Lister and

93   Aguayo 1992), thus reducing food availability for insectivorous animals. Despite these conditions,

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94   multiple diurnal lizard species inhabiting SDTF court and defend their territory during the dry

95   season (Valdéz-González and Ramírez-Bautista 2002; Bustos-Zagal et al. 2011; Granados-

96   González et al. 2015). In addition to natural seasonal defoliation, SDTF is one of the most

97   anthropized ecosystems on Earth due to deforestation and its transformation into agricultural

98   fields and grazing land (Mesa-Sierra et al. 2022). These anthropogenic disturbances create a

99   landscape with variable vegetation cover where different individuals, depending on the location of

100   their home ranges, experience different environmental conditions during the same dry season.

101   *Sceloporus ochoterenae* is a disturbance-tolerant insectivorous lizard that inhabits SDTF,

102   including open sites (Saldaña-de la Riva 1987). It defends territories during the dry season

103   (Bustos-Zagal et al. 2011), which makes it an appropriate model to test the trade-off between

104   territorial and thermoregulatory behaviors. Similar to many species of lizards (Martins 1993),

105   including sympatric species of the same genus (Bussjaeger 1971), males of *S. ochoterenae*

106   perform mobile visual signals, including push-ups, during their reproductive season in order to

107   court and defend their territory. Its reproductive season occurs from the end of the dry season

108   (May) to the middle of the rainy season (July; Bustos-Zagal et al. 2011). During the dry season,

109   SDTF lizard species are less active (Lister & Aguayo 1992; García et al. 2010), seek cooler

110   microhabitats more frequently, and thus have lower metabolic rates (Christian et al. 1996, 2003)

111   than during the rainy season, allowing them to conserve water and energy. For example, *S.*

112   *ochoterenae* shelters in shady spots or crevices to decrease its body temperature during its active

113   hours.

114   Since deforestation increases both temperature (Valenzuela-Ceballos et al. 2015) and

115   visibility in the habitat (Ferreira and Faria 2021), ectotherms are at greater risk of overheating and

116   predation in more deforested sites. Thus, ectotherms are expected to perform thermoregulatory and

117   antipredatory behaviors more frequently in more deforested territories at the expense of other

118   fundamental behaviors such as territorial defense, for example, occupying shady spots and

119   performing push-ups less frequently. Nonetheless, in order to ensure reproduction, resident male

120   ectotherms (e.g., *Uca pugilator*, *Eumeces laticeps*) in open sites tend to court females even at the

121   risk of overheating (Allen and Levinton 2014) and deter intruders even in the face of potential

122   predators (Cooper 1999) during their mating season. Thus, under the hypothesis of a temporal

123   trade-off between territoriality and thermoregulation, we expected that when using shady spots to

124   thermoregulate, *S. ochoterenae* loses opportunities to defend its territory, and that this trade-off is

125   more intense the lower the vegetation cover (and thus the higher the ambient temperature) in its

126   territory.

127   In this study, we explore the interactions between vegetation cover, microclimate

128   temperature, and the presence of conspecific intruders with the possible trade-off between the time

129   that territorial males of *S. ochoterenae* spent performing push-ups (as a proxy for territorial

130   behaviors) and spent sheltering in the shade (as a proxy for thermoregulatory behaviors) during

131   their mating season in the dry season of a SDTF. To do this, we carried out a field study in which

132   we recorded the time spent by different males doing push-ups and sheltering in shady spots in

133   territories that varied in vegetation cover and microclimate temperature. Using these data, we first

134   tested the assumption that males are more likely to perform push-ups when they are in sunny spots

135   compared to when they are in shady spots (*sensu* Bian et al. 2019; based on the hypothesis that

136   displaying in the open increases the effectiveness of their territorial signals, as described in Bian et

137   al. 2019; Fleishman and Font 2019). Second, we evaluated the existence of a negative relationship

138   between the time males spent doing push-ups and their time spent in shady spots, which would

139   support the existence of a temporal trade-off between the two behaviors (*sensu* Garland et al.

140   2022). Third, we used confirmatory path analysis to explore the relationships among vegetation

141   cover, microclimate temperature, and the presence of conspecific intruders and their effects on the

142   dynamics of the territoriality-thermoregulation trade-off, and to determine which of the two behaviors

143   was limiting the trade-off.

144   In the confirmatory path analysis, we evaluated three alternative general hypotheses of the

145   effects of the predictors on the time focal males performed push-ups and sheltered in shady spots

146   (Fig. 1). The first hypothesis proposed that in territories with less vegetation cover, the microclimate

147   temperature increases, which increases the risk of overheating, so males prioritize sheltering in

148   shady spots at the expense of time performing push-ups (Fig. 1 A–C). The second hypothesis

149   proposes that in territories with less vegetation cover, the microclimate temperature increases,

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150 which increases the visibility and body temperature of focal males, such that males spend more

151 time doing push-ups at the expense of time sheltering in shady spots (Fig. 1 D–F). The third

152 hypothesis proposes that the effect of the vegetation cover on the trade-off is not due to its effect on

153 thermoregulation, but rather on antipredatory behaviors; in territories with less vegetation cover,

154 focal males are more visible to potential predators, so males prioritize sheltering in the shade as an

155 antipredatory (rather than thermoregulatory) behavior, at the expense of time spent performing

156 push-ups (Fig. 1 G–I). Within each of these general hypotheses, we considered three variations,

157 resulting in nine total models (Fig. 1). In the first variation of each general model, the behaviors of

158 focal males vary with respect to vegetation cover and/or microclimate temperature only (A, D, G); in

159 the second, with respect to the above factors plus an increase in push-ups by focal males with

160 increasing time present of a conspecific intruder (B, E, H); and in the third, in addition to the above

161 factors, the vegetation cover and/or microclimate temperature affected the presence of intruder

162 males in the same way as the focal male (C, F, I; Fig. 1). In addition to exploring the ecology and

163 selection regime of this species, a better understanding of the dynamics and limiting factors of this

164 trade-off will provide information that could have important implications in the context of global

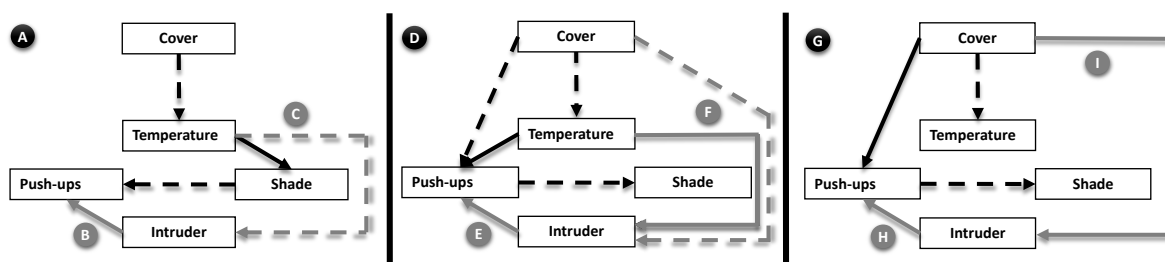165 warming and anthropogenic loss of vegetation cover.

166

167

168 **Fig. 1** Diagrammatic models illustrating the causal relationships predicted under three alternative

169 general hypotheses about the effect of the vegetation cover in the territory of focal males on the

170 potential trade-off between their time spent performing push-ups (Push-ups) and sheltering in shady

171 spots (Shade). The direction of the arrows denotes the direction of causality of the relationships.

172 Solid arrows denote positive relationships and dashed arrows indicate negative relationships. The

7

173   three general hypotheses are as follows: in territories with lower vegetation cover, focal males either

174   (A) prioritize thermoregulation to minimize their risk of overheating; (D) prioritize performing push-

175   ups to defend their territories; or (G) prioritize time in the shade to minimize their risk of predation.

176   For each general hypothesis, three alternative models were considered. The first alternative models

177   considers only the relationships between the behaviors of the focal male, the vegetation cover

178   (Cover) and the microclimate temperature (Temperature; black lines; A, D, G). The second, in

179   addition to those relationships, considers that the presence of a conspecific intruder (Intruder)

180   increases the focal male's time performing push-ups (grey lines; B, E, H). The third, in addition to

181   the previous relationships, the intruder is affected by the vegetation cover and/or the microclimate

182   temperature in the same way as the focal male (grey lines; C, F, I). These general hypotheses and

183   alternative models are described in more detail in the Introduction section.

184

185   **Methods**

186   *Study site.* The study site is centered at coordinates 18°32'47.9"N, 98°56'43.9"W at 1,200 masl,

187   within the ejido of El Limón in the Sierra de Huautla Biosphere Reserve, in south-central Mexico.

188   The average annual temperature is 22.8 ± 1.87°C (average ± standard deviation), and annual

189   rainfall is 877.3mm (SMN 2000). The dry season occurs between November and May, and the

190   months with the highest mean monthly temperature are April and May (25.75 ± 0.07°C) (SMN

191   2000). Eighty-eight percent of the annual rainfall occurs from June–October (SMN 2000). The most

192   widespread vegetation type is seasonally dry tropical forest (SDTF; CONANP 2005). In 2005, 56%

193   of the territory of El Limón was occupied by forests in conserved status, 19% in disturbed status,

194   12% by vegetation in secondary succession, and 13% by constructions and agricultural fields (De

195   Leon-Ibarra 2005). The dominant trees in this ecosystem are *Acacia cochliacantha*, *A. farnesiana*,

196   *Ipomoea pauciflora*, and *Mimosa benthamii* (Martinez-Garza et al. 2011).

197   *Study species. Sceloporus ochoterenae* is endemic to the Balsas River Basin in

198   southwestern Mexico, distributed from 520–2,134 masl, in SDTF and temperate forests (Saldaña-de

199   la Riva 1987; Bustos-Zagal et al. 2011). *Sceloporus ochoterenae* is an oviparous (Bustos-Zagal et

200   al. 2011) diurnal species that tolerates dry and warm environments (Saldaña-de la Riva 1987). It

201   occupies the ground, rocks, shrubs, and logs (Saldaña-de la Riva 1987). *Sceloporus ochoterenae* is

202   a thermoregulatory lizard; two different populations maintained an average field body temperature

203   of 34.1°C, which did not differ between sexes or vary as a function of body size (Lemos-Espinal et

204   al. 1997).

205   *Experimental design*. The study period was from April–May, which includes the warmest

206   period of the year (SMN 2000) and corresponds to the beginning of reproductive investment in *S.*

207   *ochoterenae* males (Bustos-Zagal et al. 2011). We walked potential *S. ochoterenae* habitat from

208   9h–18h, an interval that encompasses the activity hours reported for the species (Saldaña-de la

209   Riva 1987). We alternated the direction and starting point of these walks to avoid confounding the

210   sampling time with the vegetation cover of the territories; after the sampling period, we verified that

211   there was no significant relationship between these variables (Pearson r= 0.12, P= 0.4417).

212   During the walks, we searched for males that were performing the territorial push-up display

213   (Fleishman and Font 2019). Upon sighting a displaying male, the observer (IVE) moved more than

214   8m away from the focal male, covered himself with a camouflage pattern fabric, and waited 5 min

215   for the focal male to habituate. The observer recorded the activity of the focal male with binoculars

216   using 0/1 recording at 1-minute intervals (Dawkins 2007) over a 30min period (similar to other

217   observational studies in lizards, e.g., Stamps 1977; Anderson and Karasov 1981; Stapley 2006).

218   Using two categories, we estimated the time spent on territorial and thermoregulatory behaviors by

219   counting the number of intervals during which the focal male performed push-ups (=1) and occupied

220   shady spots (=1), respectively. Given that in lizards the presence of a conspecific intruder implies

221   the risk of losing the territory (Díaz-Uriarte 1999, 2001) and can evoke a stronger territorial

222   response than when no intruder is present, we also recorded the number of intervals during which

223   an intruder was visible within a 3m radius of the focal male. Since the reproductive success of male

224   lizards is positively related to the number of females within their territory and to the number of

225   copulations (Lebas 2001; Haenel et al. 2003), we also recorded the number of intervals during

226   which a female was present within a radius of 3m of the focal male and the number of copulations

227   during the entire test. However, at the end of the sampling, we only recorded the presence of

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228 females in three tests, and we did not observe copulations during any test. Since the sample size

229 was insufficient to analyze this variable specifically, we eliminated these three tests to avoid the

230 potential confounding effect. If the focal male disappeared from sight, we excluded that interval from

231 the test; if he disappeared for more than 10 continuous intervals, we abandoned that territory and

232 began the search for another male. We could repeat the test in the territories with incomplete tests,

233 restarting the test.

234   After the observation period ended, we recorded the percent vegetation cover in the

235 territory by taking a vertically oriented hemispherical photograph 50cm above the ground at the

236 point where we initially sighted the focal male. We processed the hemispherical photographs with

237 the software Gap Light Analyzer (Frazer et al. 1999). The vegetation cover quantified was used as

238 an explanatory variable in the path analysis, as well as to calculate the microclimate temperature

239 (see the following paragraph). After taking the hemispherical photograph, we recorded the

240 geographic coordinates of the territory and marked it with flagging tape placed ~8m from the sight

241 point to avoid repeating the test at that site.

242   To estimate the thermal conditions in the territory of each focal male, we calculated the

243 microclimate temperature (°C) using the NichemapR micro_ncep subroutine (Kearney et al. 2020).

244 We ran this model for the geographic coordinates of each territory; for the model parameters, we

245 input the mating season of the species as the date range of the analysis (01-April-2021 to 31-May-

246 2021), the activity hours of the species (9h–18h) as the hour range, the percentage of vegetation

247 cover quantified from the hemispherical photographs as the percent shade, the leaf area index at

248 1.5 (used for SDTF during the dry season; Maass et al. 1995), the albedo at 0.24 (Barradas &

249 Adem 1992), and the leaf angle quotient at 0.

250   *Statistical analysis*. The sample size was 36 focal males. First, we tested the assumption

251 that males were more likely to perform push-ups when in sunny spots versus when in shady spots.

252 For this, we performed a generalized linear mixed model where the sampling unit was the 1 min

253 interval, the binomial response variable was whether the male performed push-ups or not, and the

254 explanatory variable was whether or not the male was in the shade during that interval. The identity

10

255 of the focal male was included as a random variable to avoid pseudoreplication. Second, we

256 evaluated the existence of a negative relationship (which supports the existence of a trade-off)

257 between performing push-ups and occupying shady spots. To do this, we used a generalized linear

258 model with a Poisson error distribution and log link function to determine whether the number of

259 intervals during which the focal males performed push-ups was negatively related to the number of

260 intervals spent in shady spots during the test. We included the logarithm of the number of intervals

261 recorded per period as an offset to account for variation in the total test duration due to missing

262 intervals for some individuals.

263 Third, we used confirmatory path analysis to compare among the nine alternative proposed

264 models of causal relationships among the percentage of vegetation cover, microclimate

265 temperature, time with intruder present, and time during which focal males performed push-ups and

266 sheltered in shady spots (Fig. 1). We assessed the consistency between each causal model and

267 the data using the directional separation method (d-sep; Shipley 2000). This method consists of

268 generating a directional acyclic diagram (DAG) for each model of causal relationships, extracting

269 the conditional independences of the DAG, applying a hypothesis test for each conditional

270 independence, extracting their null probabilities, and generating a combined null probability for each

271 DAG based on Fisher's combined test (Shipley 2013). If the combined null hypothesis is not

272 rejected, it means that the causal relationships posed in the DAG are consistent with the data.

273 For the hypothesis tests, we performed a Poisson regression whenever the response

274 variable was the number of intervals in each test (including the logarithm of the number of intervals

275 recorded by period as an offset to compensate for differences in the total number of intervals

276 recorded). We used a quasipoisson distribution because there was overdispersion in our data. We

277 performed a simple linear regression when the response variable was continuous (microclimate

278 temperature). We then defined the most consistent DAG with the data using the combined

279 information criterion (CIC; Gonzalez-Voyer & von Hardenberg 2014). Since the number of

280 parameters of each DAG (n=8) exceeded the quotient of the number of tests (n=36) divided over 40

281 (numerical constant), we used the CIC corrected for small sample sizes (CICc; Johnson & Omland

282   2004). We utilized R to run our statistical tests and figures (R Core Team 2020). The electronic

283   supplementary material is available at (Valencia-Esquivel et al. 2023).

284   **Results**

285   The odds of performing push-ups decreased by 16.2% when males were in shady spots compared

286   to when they were in sunny spots (binomial GLMM; fixed effect, -1.548 -1.821 ± 0.325 [Intercept,

287   logit ± SE]; random effect [id of focal male], 1.522 ± 1.234 [variance ± SD]; z= -5.606, P= <0.001).

288   This confirmed that focal males were more likely to perform push-ups in the sun than in the shade.

289   We found a negative relationship between the time focal males spent performing push-ups

290   and the time they spent sheltering in shady spots. The proportion of the total test period that focal

291   males performed push-ups decreased by 7% for each additional interval they spent sheltering in the

292   shade (GLM Poisson, -1.033 -0.074 ± 0.015 [intercept, log(β) ± SE], t= -4.95, P= <0.001; Fig. 2). It

293   is important to note that this relationship was not an artifact of exclusivity between the two

294   behavioral categories (*sensu* Garland et al. 2022), since push-ups and sheltering in shade spots

295   were not mutually exclusive conditions in the behavioral scoring (i.e., a focal male could both

296   perform push-ups and be in the shade during the same interval).

297

298   According to confirmatory path analysis, all DAGs except C had a combined null probability

299   >0.05; that is, they were accepted by the d-sep method. DAG F had the lowest CICc value and,

300   therefore, was the most consistent with the data (Table 1). The other models had substantially less

301   support (ΔCIC$_\mathbf{c}$> 16 for the other models; Table 1).

302

303   DAG F indicates that the territories with less vegetation cover presented higher

304   microclimate temperatures (linear regression, 12.795 -0.186 ± 0.061°C (Intercept, β ± SE); t= -3.06,

305   P= 0.0043; Fig. 3). Focal males spent more time performing push-ups in territories with less

306   vegetation cover (GLM Poisson, -0.096 -0.056 ± 0.018 (Intercept, log(β) ± SE); t= -3.09, P= 0.0040)

307   and higher microclimate temperature (GLM Poisson, -12.085 +0.302 ± 0.113 (Intercept, log(β) ±

12

308   SE); t= 2.67, *P*= 0.0117). Focal males that spent more time performing push-ups spent less time

309   sheltering in shady spots (GLM Poisson, -0.073 -0.144 ± 0.029 (Intercept, log(β) ± SE); t= -4.93, *P*=

310   <0.001). The time focal males spent performing push-ups increased with increasing time that an

311   intruder was present (GLM Poisson, -2.214 +0.317 ± 0.112 (Intercept, log(β) ± SE); t= 2.84, *P*=

312   0.0077). Intruders were affected by the habitat characteristics of the focal territory; there were more

313   intervals during which an intruder was present in the territories with lower vegetation cover (GLM

314   Poisson, -1.095 -0.093 ± 0.039 (Intercept, log(β) ± SE); t= -2.38, *P*= 0.0231) and higher

315   microclimate temperature (GLM Poisson, -43.402 +1.140 ± 0.245 (Intercept, log(β) ± SE); t= 4.66,

316   *P*= <0.001; Fig. 3).

317

318   **Discussion**

319   In this study we tested the existence of a temporal trade-off between territorial and thermoregulatory

320   behaviors in territorial males of *S. ochoterenae* during their mating season in the dry season of a

321   SDTF. We first tested and confirmed the assumption that territorial males of *S. ochoterenae* display

322   territorial behaviors (e.g., push-ups) more frequently in sunny spots than in shady spots. We then

323   evaluated whether there was a negative relationship between these territorial and thermoregulatory

324   behaviors in focal males. We found a clear negative relationship, which is consistent with the

325   existence of a trade-off. Finally, we explored the effects of vegetation cover, microclimate

326   temperature, and the presence of an intruder in the territory on the dynamics of the trade-off and

327   determined whether territorial or thermoregulatory behavior (or neither) acted as the limiting factor

328   in the trade-off. We found that territories with less vegetation cover had higher microclimate

329   temperatures, where focal males spent more time performing push-ups at the expense of the time

330   spent sheltering in shady spots. Focal males spent more time performing push-ups the longer an

331   intruder was present, and intruders were also affected by the characteristics of the territory,

332   spending more time in territories with less vegetation cover and higher microclimate temperatures.

333

334   *Territoriality-thermoregulation trade-off*

335   Life history theory predicts that lifetime reproductive success is maximized by optimizing the

336   allocation of resources among self-maintenance, growth, and reproduction across all of an animal's

337   different life stages, such that this allocation is shaped by natural selection. We demonstrated the

338   existence of a temporal trade-off between territoriality and thermoregulation in a terrestrial species

339   under hot conditions, where the main thermal pressure is to cool off rather than to warm up. A

340   similar trade-off has been described in two semi-aquatic animals (Allen and Levinton 2014;

341   Bohórquez-Herrera et al. 2014). Male intertidal crabs (*Austruca mjoebergi*) endured high

342   temperatures at the surface rather than sheltering underground in order to court potential mates

343   (Darnell et al. 2020), while male sea lions (*Zalophus californianus*) traversed high temperatures on

344   the beach rather than cooling off in the water to ward off intruders from their harem and stop fights

345   between females (Carey 2010; Bohórquez-Herrera et al. 2014).

346   The causal relationships most consistent with our data, as determined by confirmatory path

347   analysis, showed that territorial males performed push-ups at the expense of sheltering in the

348   shade (Model F). Thus, in our system, the strategy of focal males is apparently to prioritize territorial

349   behaviors during their mating season—because push-ups allow these lizards to defend their

350   territories and to court (Martins 1993; Sheldahl and Martins 2000)—even though this likely

351   increased the risk of overheating or being depredated (Fleishman and Font 2019). This is

352   consistent with the previously mentioned examples of the territoriality-thermoregulation trade-off in

353   crabs (Darnell et al. 2020) and sea lions (Carey 2010). However, it should be noted that this was at

354   a specific time of year, phenological stage, and biological context and may not be the case at other

355   times or under other circumstances. Given that reproductive effort cannot be sustained indefinitely,

356   the other two general hypotheses could occur during the pre or post-mating season of focal males,

357   when they should decrease their reproductive effort in order to increase the investment in self-

358   maintenance. We expect that similar territoriality-thermoregulation trade-offs could occur in other

359   ectothermic species inhabiting hot-dry ecosystems.

360   We expected that males would maximize the efficiency of their signals by performing their

361   push-up displays in open, sunny places where they are most visible (Martín and López 1999; Meek

362   and Avery 2008; Carter et al. 2010), since mobile visual signals are costly in terms of energy (Zhu

14

363   et al. 2020) and time (Allen and Levinton 2014). Our data supported this prediction, showing that

364   males were more likely to perform push-ups while in sunny spots; there was a 3.4% chance that

365   males would perform push-ups during a given interval in the shade, compared to a 21.3% chance

366   when in the sun. Our results are consistent with two previous studies in which male lizards occupied

367   sunny spots more frequently when engaged in mating activities (Meek and Avery 2008; Howells

368   2013). In one, territorial male lizards (*Physignathus lesueurii*) occupied sunny spots more frequently

369   than non-territorial males during the mating season (Meek and Avery 2008). In the other, male

370   lizards (*Sceloporus undulatus*) used sites with less vegetation cover than females during the mating

371   season, but with more vegetation cover than females in the post-mating season (Howells 2013).

372   This suggests that occupying sunny locations is specifically linked to male reproductive behaviors.

373   There is evidence of other temporal trade-offs in which lizards prioritize reproduction over self-

374   maintenance, such as in reproductive versus antipredatory behaviors. For example, territorial male

375   *Agama planiceps*, *Eumeces laticeps*, *Psammodromus algirus*, and *Sceloporus virgatus* allow

376   predators to approach to a closer distance before fleeing to shelter when females (Cooper 1999;

377   Martín and López 1999) or intruders are present (Cooper 1999; Cooper and Wilson 2007). In our

378   study, territorial males prioritized territorial behaviors in sunny spots over avoiding potential

379   overheating during their mating season, especially when an intruder was present. This is similar to

380   intertidal crabs (Darnell et al. 2020) and sea lions (Bohórquez-Herrera et al. 2014). In both the

381   territorial-antipredation and territorial-thermoregulation trade-offs, focal males chose not to retreat to

382   shady-cool refuges where they would be unable to protect their territories or attract females. The

383   decreased use of shady and cool refuges by ectotherms to escape from predators or to avoid

384   overheating during their mating season must be considered when accounting for their sensitivity to

385   the heating of their habitats. For example, multiple simulations evaluate the effectiveness of

386   thermoregulatory behaviors of terrestrial ectotherms in avoiding the lethal and sub-lethal effects of

387   overheating (Kearney 2013; Valencia-Esquivel et al. 2023). Howevre, the realism of such

388   simulations could be improved by decreasing the likelihood that simulated terrestrial organisms

389   display thermoregulatory behaviors during their mating season if this happens in the wild as in our

390   case.

391

Effect of vegetation cover and microclimate temperature on focal males and intruders

393   Vegetation cover affected the time performing push-ups in two ways. On one hand, there

394   was a direct negative effect of vegetation cover on time performing push-ups (i.e., not mediated by

395   any of the other variables included in our analyses). Focal males spent more time performing push-

396   ups in less covered territories, maybe because open (i.e., unobstructed and illuminated) territories

397   increase the effectiveness of push-ups in lizards (Bian et al. 2019). A similar relationship was found

398   in territorial males of *Anolis* lizards, which performed fewer mobile displays in sites with lower

399   visibility (i.e., more complex habitats; Johnson et al. 2010). On the other hand, there was an indirect

400   effect of vegetation cover, consisting of a negative effect of vegetation cover on microclimate

401   temperature combined with a positive effect of temperature on time spent deploying push-ups, as

402   we had proposed. More open territories are warmer than less open territories because they receive

403   a higher input of solar radiation (Tuff et al. 2016), and warmer territories allow ectotherms to reach

404   higher body temperatures (Lara-Reséndiz et al. 2022). It is possible that male lizards tolerated the

405   higher temperatures of more open territories because those territories allowed particularly high

406   effectiveness of their displays.

407   The indirect effect of vegetation cover on the time deploying push-ups, through its direct effect

408   on microclimate temperature, has a thermal limit. Vegetation cover loss increases the mean air

409   temperature of forests (Tuff et al. 2016) and reduces the number and diversity of thermal refuges

410   under the canopy (Scheffers et al. 2014). Under these circumstances, remaining in sunny spots to

411   perform push-ups could increase the focal male's body temperature. If the body temperature

412   surpasses the thermal tolerance range, performance rapidly decreases in the short term, and

413   maintaining body temperatures at or above the behavioral tolerance range in a sustained way can

414   lead to sub-lethal thermogenic effects in the short or medium term. For example, overheating can

415   accelerate the expenditure of energy reserves (Rall et al. 2010) and water loss (Pintor et al. 2016),

416   forcing the ectotherm to increase its foraging rate (Rall et al. 2010) or limiting its activities to cool

417   places (Pintor et al. 2016). However, both of these compensation strategies are likely to be

16

418   challenging in the dry season of a seasonal tropical ecosystem when vegetation cover and primary

419   productivity are lower (Lister and Aguayo 1992). In temperate and subtropical latitudes, the viability

420   of ectotherm populations may also be at risk if they consistently experience habitats that are

421   warmer than those in which they evolved (Sinervo et al. 2010; Bestion et al. 2015).

422   Intruders spent more time in territories with less vegetation cover and higher microclimate

423   temperature. This may be due to two non-exclusive reasons. First, it may suggest that habitat

424   selection in *S. ochoterenae* is under selection pressure, thus the resident male and the intruder

425   seek similar habitats. Second, intruders could more easily detect resident males in more exposed

426   territories. On the other hand, the positive relationship between the time spent by the resident male

427   performing push-ups and the time the intruder spent in the focal territory could be because the focal

428   male performed push-up displays specifically directed at the intruder in order to deter the intruder

429   and/or because the resident male responded with push-ups to push-ups performed by the intruder

430   male (we did not quantify the time the intruders spent performing push-ups).

431

432   *Effect of habitat warming on the territoriality-thermoregulation trade-off*

433   Our results suggest that territorial males of *S. ochoterenae* are currently prioritizing territorial

434   behaviors over thermoregulatory ones during their early breeding season, but this could change if

435   habitat temperature increases further. Habitat warming caused by habitat loss (Kearney 2013) and

436   climate change (Bestion et al. 2015) impacts the population viability of ectotherms because body

437   temperature affects their life histories (Adolph and Porter 1993; Anderson et al. 2011). If terrestrial

438   habitats continue to warm, reproductive costs may increase to the point that males reduce their

439   reproductive effort or even skip the reproductive event (Cruz-Flores et al. 2021). For example, when

440   the body temperature of male lizards of *Sceloporus occidentalis* (a congener of our study species)

441   exceeds their preferred temperature, they stop their territorial behaviors against intruders and start

442   thermoregulatory behaviors such as sheltering in shady spots (Engbretson and Livezey 1970).

443   Indeed, this has already been demonstrated in one of the species where the territoriality-

444   thermoregulation trade-off has been observed; the probability of aggressive interactions on land

445   between male sea lions (*Z. californianus*) for harem dominance decreases with increasing air

446   temperature beyond 30°C (Bohórquez-Herrera et al. 2014). Thus, if habitats of *S. ochoterenae*

447   continue to warm in the coming decades, it may drive males to prioritize self-maintenance (i.e.,

448   future reproduction) over current reproduction.

449   If the microclimate temperature continues to increase, and if physiological plasticity (MacLean

450   et al. 2019) and thermoregulatory behaviors (Díaz et al. 2022) are insufficient to avoid the risk of

451   overheating in sunny spots, the environment could select in favor to males restrict their push-ups to

452   the cooler diurnal hours or to shady spots. On one hand, animals can avoid the hottest hours of the

453   day by following a bimodal activity pattern (Sears et al. 2011). For example, *Phrynosoma goodei*

454   (Lara-Resendiz et al. 2014) and *Uromastyx aegyptia* (Al-Sayegh et al. 2020) avoid the hottest hours

455   at midday by concentrating their activities in the morning and evening. On the other hand, the lower

456   efficiency of mobile visual signals in shady spots can be compensated by increasing their emission

457   rate (Bian et al. 2019). However, this solution would increase the energy costs of reproduction,

458   which could lead to further competition for energy reserves between reproduction and other

459   activities. In such a case, the temporal trade-off between territorial and thermoregulatory behaviors

460   would weaken, but the energetic trade-off between territorial behaviors and other activities would

461   intensify.

462   *Conclusions*

463   In this study, we demonstrated that territorial males of *S. ochoterenae* prioritize territorial

464   behaviors over thermoregulatory behaviors during their mating season in the dry season of a

465   seasonally dry tropical forest. We must explore whether this temporal trade-off occurs in other

466   terrestrial species inhabiting hot environments and predict how this trade-off would be affected by

467   warmer temperatures due to habitat loss and climate warming, for example using computational

468   modeling. If males were to prioritize thermoregulatory over territorial behaviors in the face of habitat

469   warming, thermoregulatory behaviors could compete for energy (Fey et al. 2019), time

470   (Cunningham et al. 2021), and safety with other activities. This assessment should be prioritized for

471   terrestrial ectotherms that inhabit warm environments of tropical and subtropical latitudes because

472   they have a narrower thermal performance curve and therefore pay a higher cost for failing to

473   thermoregulate than those that inhabit cool environments of temperate latitudes (Fey et al. 2019).

484   **Declaration of interest**: The authors have no competing interests to declare that are relevant to the

485   content of this article.

486   **Ethical approval:** This article does not contain any studies with human participants or manipulating

487   animals by any of the authors.

488   **Consent to participate:** Not applicable.

489   **Consent for publication:** Not applicable.

490   **Availability of data and material:** The dataset is in the following link:

491   https://data.mendeley.com/drafts/582v9zkbdz.

492   **Code availability:** The R code to reproduce our statistical tests is in the following link:

493   https://data.mendeley.com/drafts/582v9zkbdz.

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TABLES

Table 1 Results of the d-sep method applied to the nine alternative DAGs. For each DAG, the table contains the result of Fisher's combined test (Fisher's C), the degrees of freedom (df), the combined null probability (P) corresponding to Fisher's C, the number of parameters, the value of the information criterion corresponding to Fisher's C (CICc), and the difference in CICc of each model relative to the most supported model (ΔCICc). Model C (italics) had a significant combined null probability, so it was discarded as it was inconsistent with the data, and its CICc and ΔCICc are not reported. The DAG values most consistent with the data (F) are in bold type

DAG	Fisher's C	df	P	Parameters	CICc	ΔCICc
A	43.76	14	0.97	8	65.09	27.70
B	32.17	12	0.88	8	53.50	16.11
C	*8.68*	*10*	*0.01*	*9*	—	—
D	38.81	12	0.97	8	60.14	22.75
E	34.36	10	0.98	8	55.69	18.30
F	**12.47**	**6**	**0.59**	**9**	**37.39**	**0.00**
G	41.77	14	0.95	8	63.10	25.71
H	35.01	12	0.93	8	56.35	18.96
I	29.43	10	0.92	9	54.35	16.96

Figure legends

Fig. 1 Diagrammatic models illustrating the causal relationships predicted under three alternative general hypotheses of the effect of the vegetation cover in the territory of focal males on the potential trade-off between their time spent by performing push-ups (Push-ups) and sheltering in shady spots (Shade). The direction of the arrows denotes the direction of causality of the relationships. Solid arrows denote positive relationships and dashed arrows indicate negative relationships. The three general hypotheses are as follows: in territories with lower vegetation cover, focal males either (A) prioritize thermoregulation to minimize their risk of overheating; (D) prioritize performing push-ups to defend their territories; or (G) prioritize time in the shade to minimize their risk of predation. For each general hypothesis, three alternative models were considered. The first considers only the relationships between the behaviors of the focal male, the vegetation cover (Cover) and the microclimate temperature (Temperature; black lines; A, D, G). The second, in addition to those relationships, considers that the presence of a conspecific intruder (Intruder) increases the focal male's time performing push-ups (grey lines; B, E, H). In the third, in addition to the previous relationships, the intruder is affected by the vegetation cover and/or the microclimate temperature in the same way as the focal male (grey lines; C, F, I). These hypothesis and alternative models are described in more detail in the Introduction section

Fig. 2 Relationship between the time males spent in shady spots and time spent performing push-ups. The proportion refers to the number of intervals in which the corresponding behavior was observed divided by the total intervals in the observation period for each focal male. The 36 focal males are represented by the points, and the gray shaded area indicates the 95% confidence interval around the trend line from a Poisson regression (black curve; solid line significant at $P < 0.001$)

Fig. 3 Causal relationships of the F model, the DAG that was most consistent with the data. Boxes represent the percentage of vegetation cover (Cover), microclimate temperature (Temperature), number of intervals with an intruder present (Intruder), and number of intervals during which focal males performed push-ups (Push-ups) and sheltered in shady spots (Shade). The direction of the arrows denotes the direction of the causal relationship, and arrow thickness is proportional to the magnitude of the relationship. Solid lines denote positive relationships and dashed lines negative relationships. The numbers are the percentage change expected in the response variable with a one-unit increase in the predictor (i.e., the coefficient of the Poisson regression transformed to express it on the original scale of the data), except for the Temperature-Cover relationship, which is the coefficient from the simple linear regression. The number of asterisks denotes the level of significance (* $P< 0.05$, ** $P< 0.01$, *** $P< 0.001$). Full numerical results can be found in the Results section
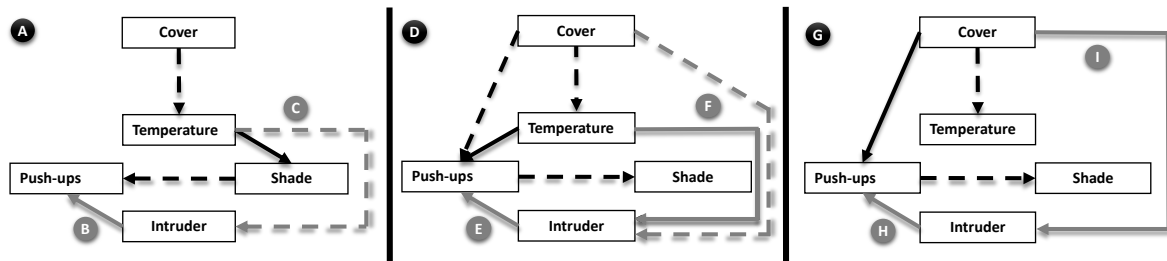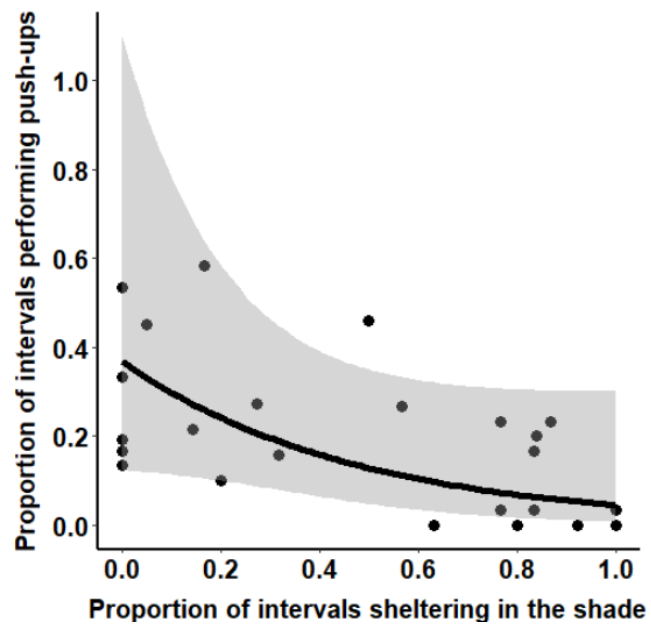
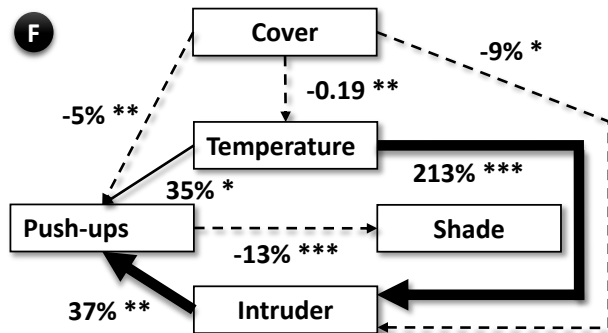**Fig. 1**

Fig. 2

Fig. 3

Table 1 Results of the d-sep method applied to the nine alternative DAGs. For each DAG, the table contains the result of Fisher's combined test (Fisher's C), the degrees of freedom (df), the combined null probability (P) corresponding to Fisher's C, the number of parameters, the value of the information criterion corresponding to Fisher's C (CICc), and the difference in CICc of each model relative to the most supported model (ΔCICc). Model C (italics) had a significant combined null probability, so it was discarded as it was inconsistent with the data, and its CICc and ΔCICc are not reported. The DAG values most consistent with the data (F) are in bold type

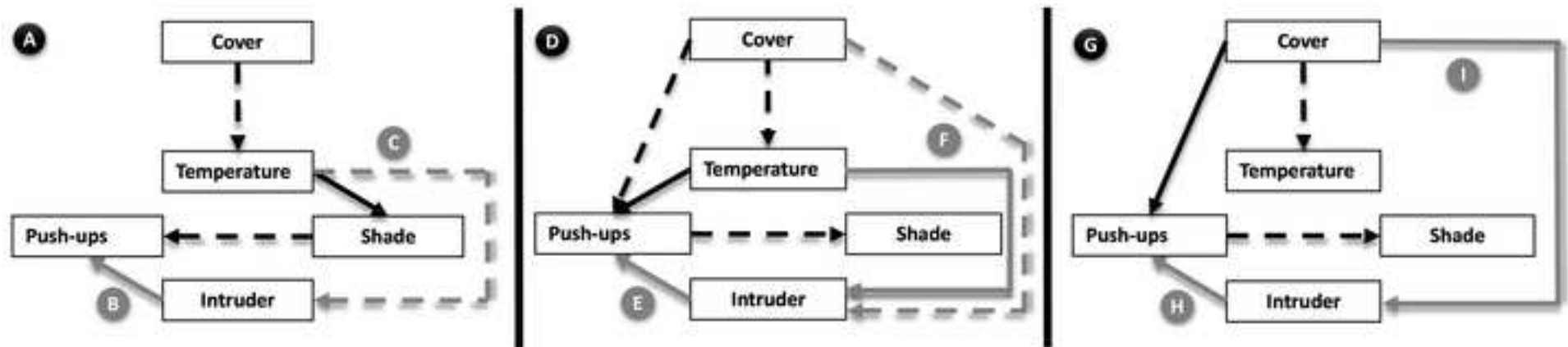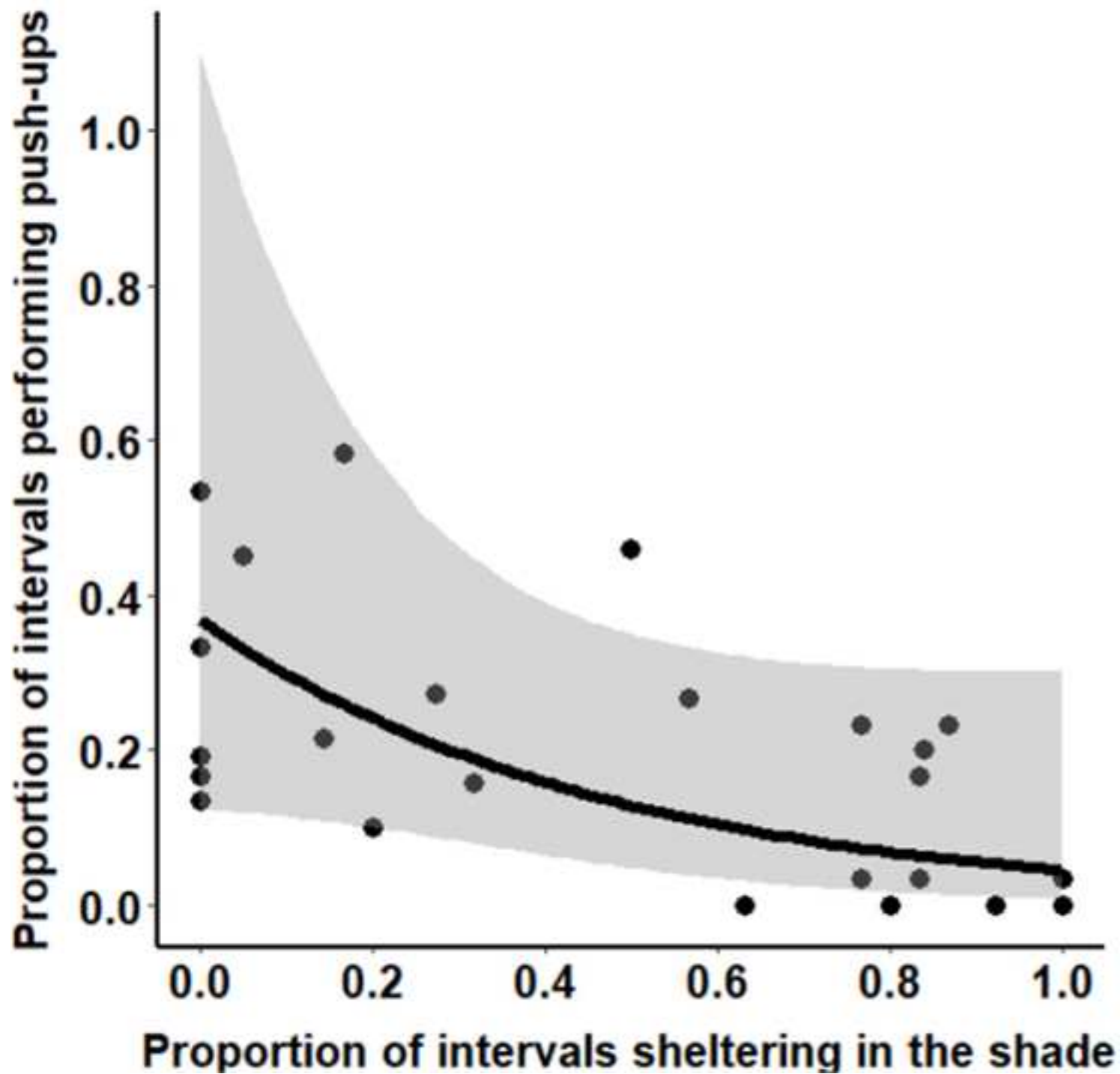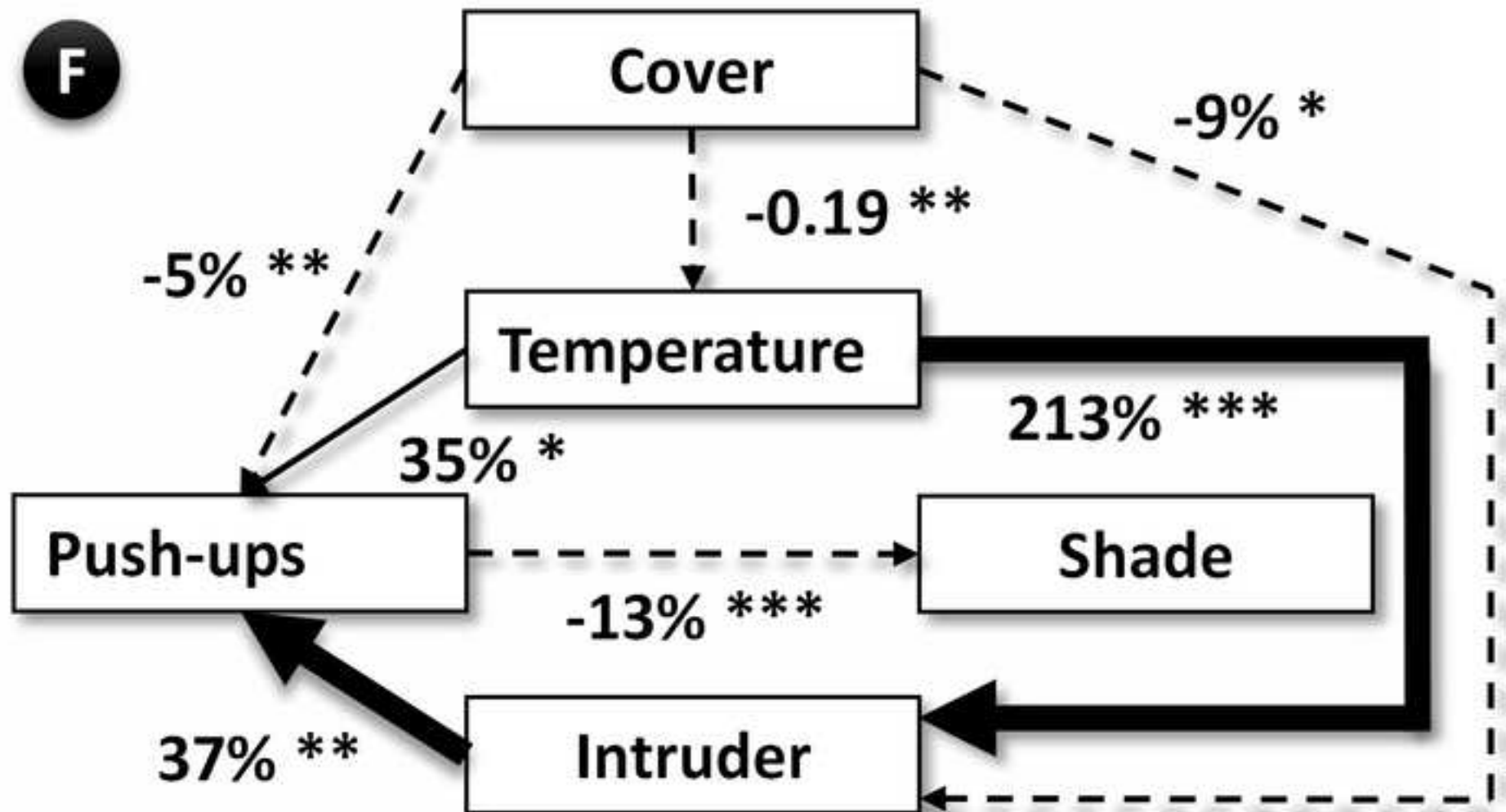| DAG	Fisher's C	df	P	Parameters	CICc	ΔCICc
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B	32.17	12	0.88	8	53.50	16.11
C	*8.68*	*10*	*0.01*	*9*	—	—
D	38.81	12	0.97	8	60.14	22.75
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F	**12.47**	**6**	**0.59**	**9**	**37.39**	**0.00**
G	41.77	14	0.95	8	63.10	25.71
H	35.01	12	0.93	8	56.35	18.96
I	29.43	10	0.92	9	54.35	16.96

Figure 1

Figure 2

Figure 2

Figure 3

Figure 3

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