

The use of bat houses as day roosts in macadamia orchards, South Africa

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Despite the valuable ecosystem service of pest control provided by bats, an ever growing human population and agricultural intensification has led to a worldwide threat of extinction to about one quarter of all bat species. The loss of roost sites is one of the major drivers of this decline, while the roost site preference and artificial roost site use by African bat species is little understood. In this study, we focus on the preference of artificial roost sites by insectivorous bats in macadamia orchards in South Africa (Levubu, Limpopo). From June 2016 to July 2017 we scanned 31 bat houses, mounted on poles on six macadamia orchards, for bats or any other occupants such as wasps, birds and bees. Twenty-one multi-chambered bat houses of three different designs (6-Chambered, Nursery and Old George bat houses) were erected on poles, in sets of three. Additionally, five Rocket boxes, four bat houses, in sets of two (black and white) and one colony bat house were erected. Bats were counted and visually identified to family or species level. From December 2016 to end of March 2017, three IButtons were installed to record temperature variation between one set of three bat houses. We related the occupancy of bat houses in the different types of houses to the environmental variables distance to water, altitude and height of bat house as well as the difference in mean temperature between the set of three bat houses. The central bat house in the set of three and the black bat house in the set of two had a significantly positive effect on bat house occupancy. There was a significant difference in the mean temperature between the houses in the set of three, with a significant difference in temperature of 0.46°C between the central and the first bat house. The Yellow-bellied house bat (*Scotophilus dinganii*) was by far the most recorded and the only species observed to co-habitat a bat house with other animal species, in particular honeybees. Our study might confirm previous assumptions in that the microclimate of bat houses, respectively their insulation, sun exposure and color appear to be important factors, positively influencing bat house occupancy. The two preferred bat

houses in our study were the black, in the set of black and white, as well as the central house, in the set of three. In conclusion from the different bat houses tested in this study, the designs we assume the warmest and best insulated, which were mounted freestanding on poles and in sets worked best to attract bat house occupancy in northern South Africa. Further research on the preferred microclimate of bat species especially on the response to temperature variation within bat houses, co-habitation of bat houses and displacement behavior as well as the potential importance of altitude and distance to water is needed.

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20

21 Abstract

22 Despite the valuable ecosystem service of pest control provided by bats, an ever growing human
23 population and agricultural intensification has led to a worldwide threat of extinction to about
24 one quarter of all bat species. The loss of roost sites is one of the major drivers of this decline,
25 while the roost site preference and artificial roost site use by African bat species is little
26 understood. In this study, we focus on the preference of artificial roost sites by insectivorous
27 bats in macadamia orchards in South Africa (Levubu, Limpopo).

28 From June 2016 to July 2017 we scanned 31 bat houses, mounted on poles on six macadamia orchards,
29 for bats or any other occupants such as wasps, birds and bees. Twenty-one multi-chambered bat
30 houses of three different designs (6-Chambered, Nursery and Old George bat houses) were
31 erected on poles, in sets of three. Additionally, five Rocket boxes, four bat houses, in sets of two
32 (black and white) and one colony bat house were erected.

33 Bats were counted and visually identified to family or species level. From December 2016 to end of
34 March 2017, three IButtons were installed to record temperature variation between one set of three
35 bat houses. We related the occupancy of bat houses in the different types of houses to the
36 environmental variables distance to water, altitude and height of bat house as well as the
37 difference in mean temperature between the set of three bat houses. The central bat house in
38 the set of three and the black bat house in the set of two had a significantly positive effect on bat
39 house occupancy. There was a significant difference in the mean temperature between the
40 houses in the set of three, with a significant difference in temperature of 0.46°C between the
41 central and the first bat house. The Yellow-bellied house bat (*Scotophilus dinganii*) was by far the
42 most recorded and the only species observed to co-habitat a bat house with other animal species,
43 in particular honeybees. Our study might confirm previous assumptions in that the microclimate
44 of bat houses, respectively their insulation, sun exposure and color appear to be important factors,
45 positively influencing bat house occupancy. The two preferred bat houses in our study were the
46 black, in the set of black and white, as well as the central house, in the set of three. In conclusion
47 from the different bat houses tested in this study, the designs we assume the warmest and best
48 insulated, which were mounted freestanding on poles and in sets worked best to attract bat
49 house occupancy in northern South Africa. Further research on the preferred microclimate of bat

50 species especially on the response to temperature variation within bat houses, co-habitation of
51 bat houses and displacement behavior as well as the potential importance of altitude and
52 distance to water is needed.

54 Introduction

55 In Europe, artificial bat roosts have long been tested and reviewed to compensate for a loss of
56 natural roost sites, particularly in silviculture (Bäumler 1988; Issel&Issel 1955; Natuschke 1960;
57 Schwenke 1983). More recently, the value of insectivorous bats for agriculture and the use of
58 bat houses in agricultural landscapes has received growing attention (Boyles et al. 2011;
59 Cleveland et al. 2006; Flaquer et al. 2006; Kunz et al. 2011; Lopez-Hoffman et al. 2014; Maas et
60 al. 2013; Puig-Montserrat et al. 2015; Taylor et al., 2018; Wanger et al. 2014). Nevertheless, an
61 ever growing human population and related ongoing land use change, especially agricultural
62 intensification, has led to a worldwide threat of extinction to about one quarter of all bat species
63 (see Fig. 1.3 in Voigt & Kingston 2016; Mickleburgh et al. 2002, Tilman et al. 2011; Tscharncke et
64 al. 2012). The loss of roost sites is one of the major drivers of this decline (Mickleburgh et al.
65 2002; Park, 2015) and there is a particular lack of knowledge regarding the roost site preferences
66 of African bat species (Monadjem et al. 2009; Monadjem et al. 2010a; Taylor 2000). Given the
67 accelerating land use change from natural to agricultural landscapes especially in the third world
68 and the assumed decline in South African bat populations (Voigt & Kingston, 2016), proactive
69 management of bat populations is indispensable to sustain their long-term ecosystem services
70 (Cumming et al., 2014; Taylor et al., 2017; Tuttle et al., 2013). Proactive management of bat
71 population will require to fill existing knowledge gaps on roost site preferences for African bat
72 species and the means of successful conservation of bats in intensive agricultural systems in
73 particular (Monadjem et al., 2009; Park, 2015; Taylor, 2000).

74 Peer-reviewed studies focusing on artificial roost site use by African bat species are literally non-
75 existent and by far the most studies have been conducted in Europe followed by North America
76 and Australia (Rueegger, 2016).

77 Summarizing the studies conducted globally so far, bat species seem to have a general
78 preference for bat houses with a large volume, multi-compartments and those mounted on
79 poles or houses compared to bat houses mounted on trees (Rueegger, 2016). There also seems
80 to be a preference for bat houses build from 'woodcement' (Dodds& Bilston 2013; Gerell 1985;
81 Haensel& Tismer; 1999), although these studies are all limited to one climatic region in Europe
82 ('mild temperate/fully humid/warm summers'), according to the Köppen climate classification.

83 Generally, the microclimate of bat houses, respectively insulation, sun exposure and color seems
84 to be an important factor influencing bat house occupancy (Fukui et al. 2010; Rueegger, 2016;
85 Shek et al. 2012). Looking at different designs and colors of bat houses, studies suggest that
86 preferences also vary greatly depending on the reproductive state of females (Baranauskas
87 2009; Fukui et al. 2010; Flaquer et al. 2006; Kerth et al. 2001). Furthermore, many bat species
88 seem to be sensitive to competition for bat houses by other species, mostly by birds and social
89 bees, ants and wasps (Baranauskas 2009; Dodds& Bilston 2013; Meddings et al. 2011).

90 There is certainly a great need for research on artificial roost site use, especially in Africa, and
91 this is the first peer-reviewed study looking at the occupancy of bat houses in South Africa.
92 Successful bat house design and deployment seem to relate mostly to the climatic region and
93 bat species targeted, while the pressure of land use change and loss of roost sites is increasing.
94 The objective of this study was, therefore, to gain insight into the preference of artificial roost
95 sites by insectivorous bats in macadamia orchards in South Africa. The main research question
96 was, what are key features of occupied artificial roost sites (bat houses)?

97 We hypothesized that bat houses providing a warm microclimate and those erected close to
98 water sources will do particularly well.

99

100 **Materials and methods**

101

102 **Study area and bat house design**

103 The study was conducted in the fruit growing area of Levubu, Limpopo, South Africa, which
104 accounts for the second highest production of macadamia in the country (see Figure 1). The
105 climate in the study area is subtropical with around 1000 mm of annual rainfall. Other
106 dominant land use types other than macadamia are pecan, avocado and banana orchards as
107 well as pine and gum plantations (Taylor et al. 2017).

108 The Subtropical Fruit Association of South Africa (Subtrop) arranged for twenty-one multi-
109 chambered bat houses to be mounted on poles, in sets of three, on four macadamia orchards in
110 the Levuvhu river Valley, Limpopo, South Africa, in 2014. Every set of three houses
111 comprised one 6-Chamber bat house in the middle as well as an Old George bat house and a

112 Nursery bat house to either side (see Figure 2). Both the Nursery bat house and the Old George
113 bat house vary slightly in their chamber design. The Old George model is different from the
114 other designs, in that several of the spacers between the different chambers are set at an angle
115 (Freed&Falxa, 2010). Whereas, the Nursery bat house has four chambers getting shorter in
116 length towards the back of the house (see Figure 2). These bat houses were maintained in May
117 2016 and five two-chambered Rocket boxes (see Figure 2) were put up close to all but one set
118 of three bat houses. The freestanding rocket boxes allow the bats to move around in 360°
119 degrees within the house and choose from a range of temperatures respectively sun exposure.
120 An additional four four-chambered bat houses, in sets of two (painted black and white in order
121 to provide different microclimates), also mounted on poles and one colony bat houses were
122 erected in March 2016 on two additional macadamia orchards (see Figure 2). All bat houses are
123 constructed of wood and mounted on pine poles, also see Supplementary Table 1 for detailed
124 information.

125 As proposed for warm climates by the 'North American bat house research project', all bat
126 houses erected for this study have open bottoms (Kiser&Kiser 2004). They are also placed near
127 water sources and natural vegetation, wherever possible. Except for the colony bat house,
128 several bat houses were erected at each location, which is proposed to positively influence
129 occupancy by providing different microclimates (Sedgeley, 2001). Alternating between different
130 bat houses might also be necessary for bats to avoid predators and high ectoparasite loads
131 (Lewis, 1995; Reckardt&Kerth, 2006).

132

133 **Bat house occupancy**

134 All bat houses were scanned monthly from June 2016 to July 2017 for bats or any other occupants
135 such as wasps, birds and bees unless weather prevented access, by reflecting sunlight with
136 mirrors into the houses. This process was kept as short as possible to avoid any major
137 disturbance to occupant bats. Bats were counted and identified visually to family or species level
138 referring to Monadjem et al. (2010b) and species records of Weier et al. (2018). Bat houses
139 solely occupied by wasps or bees were cleared during maintenance in May 2016. We are
140 working under the ongoing permit (No. 001-CPM403-00010) for research on small mammals

141 from the Limpopo Department of Economic Development, Environment and Tourism. During 1st
142 of December to 20th of March 2017, three IButtons (Thermochron, DS1921G-F5) were successfully
143 installed with a tongue and sticky tape at each of the three entrances of one set of three bat houses to
144 record temperature variation between the bat houses 1.5 hourly. While scanning the houses and
145 fitting the IButtons we tried to avoid touching the bat house or the poles close to the house to
146 keep disturbance to a minimum (Tuttle et al. 2013).

147 Additionally, we recorded the distance to the closest water source (Google Earth), the cardinal
148 direction facing (Digital Compass, Axiomatic Inc.), the altitude above sea level (GPS Waypoints,
149 Bluecover Technologies) and the height on poles of each bat house.

150

151 **Data analyses**

152 All statistical analyses was conducted with R (version 3.4, R Core Team 2017). The bat house of
153 the type 'colony' was not used for analyses, as there was only one bathouse of this type.

154 The relatively small sample size of 31 bat houses (with 21 of them erected in sets of three) lead
155 to a correlation between the type of bat house and the cardinal direction the different houses
156 are facing. Additionally, not all possible combinations of the different bat house types and
157 cardinal directions are available for statistical analyses. Therefore, we fitted a model to analyze
158 the relationship of the response variable 'presence or absence of bats' and the predictor
159 variables 'type of bat house', 'altitude', 'distance to water' and 'height of the bat house' (see
160 Supplementary Table 2).

161 After testing the model for normal distribution and constant errors variance, we applied a
162 generalized linear mixed model (GLMM) with a binomial distribution (package 'lme4' by Bates
163 et al. 2015). The variables 'farm' and 'month' were used as random factors to account for
164 pseudo replication and all the numeric predictor variables were scaled. We used the dredge
165 function (package 'MuMIn' by Barton 2017) based on the lowest values of the Akaike
166 information criterion (AICc), corrected for a small-sample size, to select final models.

167 In order to analyze differences in temperature recorded between one of the sets of three
168 houses we fitted an ANOVA and used the Tukey test for multiple comparison (package 'stats' by

169 R Core Team 2017). Additionally, we used the summary statistics base function ‘tapply’ to look
170 at differences in range and mean of temperature (version 3.4, R Core Team 2017).

171

172 **Results**

173 We recorded a total of 166 individual bats within the 31 bat houses, from June 2016 to July 2017,
174 with a maximum of 5 individual bats in one bat house (DatasetS1). The highest average number of bats
175 was recorded in March and May (on average 0.53 bats per bat house), whereas the lowest average
176 numbers were recorded in August and November (0.3). We recorded Yellow-bellied house bats
177 (*Scotophilus dinganii*) on 43 occasions, small Plain-faced bats (*Vespertilionidae*) on nine occasions, Free-
178 tailed bats (*Molossidae*) on 21 occasions and Mauritian tomb bat (*Taphozous mauritanus*) on three
179 occasions (also see Supplementary Table 3).

180

181 **Type of bat house**

182 The first five models selected by dredge, analyzing the relationship of the response variable
183 ‘presence or absence of bats’ with the predictor variable(s) were all within a delta AICc of <2
184 (see Supplementary Table 2). After testing all five models, which each retained ‘type of bat
185 house’ as the only significant variable, we decided for the simplest final model (presence of
186 bats~type of bathouse).

187 The bat house occupancy on the macadamia orchards was influenced by the type of bat house,
188 in that the central bat house ($\beta=1.43$, $SE=0.41$, $p<0.001$) in the set of three and the black bat
189 house in the set of two ($\beta=2.30$, $SE=0.56$, $p<0.001$) had a significantly positive effect on the
190 presence of bats (see Table 1 and Figure 3).

191

192 **Temperature**

193 The ANOVA showed that there was a significant difference in the mean temperature values
194 between the houses in the set of three ($F_{(2,5682)} = 4.34$, $p=0.0139$), in the summer months
195 December 2016 to April 2017 (DatasetS2). A post hoc Tukey test showed that there was a
196 significant difference in temperature of 0.46°C between the second, 6-Chamber bat house, and
197 the first bat house ($p=0.016$, an Nursery bat house, and a marginal significant difference

198 between the third, Old George bat house, and the second house ($p=0.055$). The temperature
199 range was between a minimum of 12.5 and maximum of 40.5°C in the Nursery bat house and
200 between min. 12 and max. 41°C in the second and third bat house (6- Chamber and Old George
201 house). The mean temperature was the warmest in the second (central) bat house with 23.52°C
202 compared to 23.06°C in the first bat house and 23.13°C in the third bat house. The ambient
203 temperature recorded in Ratombo (about 7 km as the crow flies from the Ibuttons used in this
204 study) over the last 30 years, from December to end of March, shows a mean daily minimum of
205 18-19°C and a mean daily maximum of 27-28°C with peaks of up to 35°C in December
206 (Meteoblue, 2018).

207

208 **Other bat house occupants**

209 We observed a number of other animals occupying the bat houses in the presence and absence
210 of bats. Namely, we encountered Lesser Galago (*Galago moholi*), Tree squirrel (*Paraxerus*
211 *cepapi*) and nests which could also belong to Dormouse (*Myoxidae*), Lizards (*Lacertilia*), social
212 wasps (*Vespidae*) and Honeybees (*Apis*). We twice (May 2017 and June 2016) observed Yellow-
213 bellied house bats (*Scotophilus dinganii*) sharing a bat house with an active honeybee hive.

214

215 **Discussion**

216 From 166 individual bats observed during our study, the highest average number of bats were
217 recorded in March and May, whereas the lowest average numbers were recorded in August and
218 November. The bat house type was a significant variable influencing bat house occupancy, with a
219 preference for the black house, from the set black and white, and the 6-Chamber model, the central
220 house in the set of three. We assume that these are the two warmest houses, because of color (black)
221 and insulation (central house of three and 6-chambered) and are, therefore, the preferred types of bat
222 houses occupied by bats.

223

224 The highest (March and May) and lowest (November and August) average numbers of bats
225 recorded during our study matches the high (December to end of May) and the low (June to
226 end of November) season of pest insect species occurrence on macadamia orchards, according

227 to Weier et al. (2018). The study of Weier et al. (2018), conducted in the same study area,
228 shows that not only bat activity is nearly doubled in the high season but also that bat activity
229 increases with Hemipteran abundance. This also supports the assumption that insectivorous
230 bat species track outbreaks of insect pest species such as stinkbugs (Taylor et al. 2013; Taylor et
231 al. 2017; McCracken et al. 2012). We, therefore, suggest that colonization of bat houses in and
232 around macadamia orchards might be highest in times of high prey availability of pest insect
233 species particularly stinkbugs (see Figure 4).

234

235 Our study might confirm previous assumptions in that the microclimate of bat houses
236 respectively insulation, sun exposure and color are important factors influencing bat house
237 occupancy (Fukui et al. 2010; Kerth et al. 2001; Lourenço & Palmeirim 2004; Sedgeley, 2001; Shek
238 et al. 2012).

239 Bats generally preferred the black houses, in the set of black and white, and 6-Chamber models,
240 the central bat house in the set of three. The 6-Chamber models were mounted flanked either
241 side by other houses and had the most chambers of all erected bat houses, which provided
242 additional insulation (see Figure 2). We suggest that this insulation affected the preference by
243 bats rather than the bat house design. It would be worth investigating how occupancy changes if
244 this central bat house, the 6-Chamber model, is erected individually. However, we suggest that
245 the insulation to either side of the 6-Chamber bat house by an additional bat house and the
246 amount of chambers had a significant effect on bat house occupancy respectively microclimate.
247 It should be noted, however, that only one set of three houses was measured with Ibuttons in
248 our study and temperature deductions are based on this data. Future studies should aim at a
249 higher sample size in order to investigate possible temperature variances caused by
250 environmental factors. Because black colors absorb wavelength and therefore energy and white
251 colors reflect them, it is reasonable to assume that the black bat houses in the sets of two are
252 significantly warmer than the white bat houses. However, precise information on the differences
253 in temperature would provide further insight into the preferred microclimate of bathouses by
254 different bat species.

255 The colony bat house remained unoccupied throughout this study. In order to distinguish if this
256 is an effect of the location or the type of bat house, several colony bat houses need to be
257 erected and monitored. We also suggest that the colony bat house might have remained
258 unoccupied because it did not provide any other artificial roost sites in close vicinity so
259 alternating between different bat houses was not possible. The Rocket box design did
260 particularly well in the United States and Canada with 62% overall occupancy (Kiser&Kiser,
261 2004), therefore, occupancy of the Rocket boxes might still increase with time (Agnelli et al.,
262 2011). However, one component, which both the Rocket box and the Colony bat house are
263 missing compared to the other designs erected, is a landing patch (see Figure 2).

264

265 Yellow-bellied house bats were by far the most recorded (42 times compared to nine
266 observations of small plain-faced bats). This species is naturally tree cavity roosting but well
267 known to utilize anthropogenic structures particularly rooftops (Monadjem et al. 2010a). Given
268 the large size of Yellow-bellied house bats (weighing up to 37 grams), they might have a
269 competitive advantage over smaller bat species (Monadjem et al. 2010a). However,
270 displacement behaviour between different bat species can only be confirmed by for example
271 fitting cameras to bat houses, such as in the study of Kerth et al. (2001). Furthermore, it is not
272 yet known what effect the installation of artificial roosts have on the local community
273 composition of bats and if it might lead to displacement behaviour of rare species by common
274 species (Russo&Ancillotto, 2015).

275 The distance to water, the altitude above sea level and the height of bat houses did not
276 significantly influence bat house occupancy in our study. While water availability is known to
277 influence bat activity (Crisol-Martínez et al. 2016; Grindal et al. 1999; Rainho& Palmeirim 2011),
278 the bat houses in this study were erected within 2 to 680 meters from the closest water source,
279 all within the known home range of even small plain-faced bats (Monadjem et al. 2010b). We
280 also suggest that the distance to water might become more significant in regions that are more
281 arid than our subtropical study area. There might also be a difference in this response during the
282 dry season, which we suggest should be analyzed once a large data set becomes available. The

283 altitude above sea level did range from 607 to 932 meters in this study and did, therefore, not
284 provide a great variation in temperature.

285

286 While we observed a number of other animals in the bat houses during this study, the present
287 bat house design did not seem to attract birds such as reported by Dodds& Bilston (2013).

288 Interestingly, while there are contrasting observations on whether wasps displace bats from bat
289 houses (Rueegger, 2016), we did not observe co-habitation with wasps but with active
290 beehives. However, tree squirrel and/or dormice might be able to displace bats as we only
291 found a bat house occupied by bats with a mammal nest present once, in which case the nest
292 seemed abandoned for some time.

293 The collection of bat faecal pellets, for a parallel project on bat diet, also suggests that the
294 occupancy of bat houses is much higher than what we observed by recording the presence of
295 individual bats during our monthly visits, as we often collected faecal pellets under unoccupied
296 bat houses. While alternating between different roosts is well known especially for pregnant
297 bats (Kerth et al. 2001; Reckardt& Kerth, 2006) as well as fission and fusions behaviour
298 (Kerth&König 1999), our study focused on the use of bat houses as a day roost and different
299 occupancy numbers might be observed when conducting nightly visits.

300 As visits were conducted monthly, we could not exclude the possibility that signs of bat
301 presence such as faeces were washed away by rain or disintegrated in the sun beforehand. We
302 did, therefore, not include this in our analyses. However, this variable should be kept in mind
303 for future studies and might be a possible variable to use for studying winter roost occupancy
304 during the dry months in northern South Africa, especially if data is collected over several years.

305

306 All of the bat houses in this study are freestanding with no direct cover by trees or houses to
307 either side. While we were unable to analyze the influence of the cardinal direction respectively
308 sun exposure on bat house occupancy, we suggest that future studies should consider this
309 variable, particularly if bat houses are mounted onto the walls of houses and receive shadow
310 from at the back. It would also be ideal to, additionally, test bat houses mounted back-to-back

311 to provide additional insulation as proposed by Kiser and Kiser (2004) and control temperature
312 variation between all houses of different designs.

313 It should also be noted that we found dead bats in or under bat houses on three occasions.
314 Although we can currently not make an informed statement regarding the cause of these
315 deaths, we would like to advice caution when it comes to placing bat houses within orchards,
316 which are frequently sprayed with pesticides. We recommend to rather erect bat houses at the
317 edges of orchards, in some distance to the crops which will be sprayed.

318

319 **Conclusions**

320 From the experience gained so far in northern South Africa, the bat houses we assume the
321 warmest and best insulated, which were mounted freestanding on poles and in sets worked
322 best to attract bat house occupancy. Further research is necessary and should focus on co-
323 habitation of bat houses and displacement behavior as well as add a greater variation in
324 altitude and distance of bat houses to water. There is also a vast scope to experiment with
325 different colors, designs and position of bat houses and to look into the preferred microclimate
326 of different bat species especially their response to temperature variation within bat houses.

327

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335

336

337 **References**

- 338 Agnelli P, Maltagliati G, Ducci L, Cannicci S. 2010. Artificial roosts for bats: education and
339 research. The "Be a bat's friend" project of the Natural History Museum of the University of
340 Florence. *Hystrix the Italian Journal of Mammalogy* 22(1):215-223.
341
- 342 Bäumler W. 1988. Fledermäuse und Bilche in Nistkästen - Eine Erhebung in Bayern. *Anzeiger für*
343 *Schädlingskunde, Pflanzenschutz, Umweltschutz* 61: 149-152.
344
- 345 Baranauskas K. 2009. The use of bat boxes of two models by Nathusius' Pipistrelle (*Pipistrellus*
346 *nathusii*) in Southeastern Lithuania. *Acta Zoologica Lituanica* 19: 3-9.
347
- 348 Barton K. 2017. MuMIn: multi-model inference. R package version 1.40.0. Available
349 at <https://CRAN.R-project.org/package=MuMIn> (accessed 12 September
350 2017)
351
- 352 Boyles JG, Cryan PM, McCracken GF, Kunz TH. 2011. Economic importance of bats in
353 agriculture. *Science* 332:41-42.
354
- 355 Cleveland CJ, Betke M, Federico P, Frank JD, Hallam TG, Horn J, Lopez JD, McCracken GF,
356 Medellín RA, Moreno-Valdez A, Sansone CG, Westbrook JK, Kunz TH. 2006. Economic value of
357 the pest control service provided by Brazilian free-tailed bat in south-central Texas. *Frontiers in*
358 *Ecology and the*
359 *Environment* 4:238-243.
360
- 361 Crisol-Martínez E, Ford G., Finbarr GH, Brown PH, Wormington KR. 2016. Ecology and
362 conservation of insectivorous bats in fragmented areas of macadamia production in eastern
363 Australia. *Austral Ecology*. <https://doi.org/10.1111/aec.12478>.
364
- 365 Dodds M. and Bilston H. 2013. A comparison of different bat box types by bat occupancy in
366 deciduous woodland, Buckinghamshire, UK. *Conservation Evidence* 10: 24-28.
367
- 368 Flaquer C, Torre I, Ruiz-Jarillo R. 2006. The value of bat-boxes in the conservation of *Pipistrellus*
369 *pygmaeus* in wetland rice paddies. *Biological Conservation* 128:223-230.
370
- 371 Freed S, Falxa G. 2010. Bat Box Preference Study on Fort Lewis, Washington. Annual meeting of
372 the Washington Chapter of The Wildlife Society, Marysville. Available at
373 [http://www.cascadiaresearch.org/files/Projects/Archived_projects/Bats/BatBoxPreference_scr](http://www.cascadiaresearch.org/files/Projects/Archived_projects/Bats/BatBoxPreference_screen-view.pdf)
374 [een-view.pdf](http://www.cascadiaresearch.org/files/Projects/Archived_projects/Bats/BatBoxPreference_screen-view.pdf) (accessed 2 October 2018)
375
- 376 Fukui D, Okazaki K, Miyazaki M, Maeda K. 2010. The effect of roost environment on roost
377 selection by nonreproductive and dispersing Asian parti-coloured bats *Vespertilio sinensis*.
378 *Mammal Study* 35: 99-109.
379

- 380 Gerell R. 1985. Tests of boxes for bats. *Nyctalus (N.F.)* 2: 181–185.
381
- 382 Grindal SD, Morissette JL, Brigham RM. 1999. Concentration of bat activity in riparian
383 habitats over an elevational gradient. *Canadian Journal of Zoology* 77: 972–977.
384
- 385 Haensel J. and Tismer R. 1999. Versuchsrevier für Fledermauskästen im Forst Berlin-
386 Schmöckwitz - Ergebnisse, insbesondere zu den überwiegend vertretenen
387 Rauhautfledermäusen (Pipistrellus nathussi). *Nyctalus (N.F.)* 7: 60–77.
388
- 389 Issel B. and Issel W. 1955. Versuche zur Ansiedelung von ‘Waldfledermäusen’ in
390 Fledermauskästen. *Forstwissenschaftliches Centralblatt* 74: 193–204.
391
- 392 Kerth G. and König B. 1999. Fission, fusion and nonrandom associations in female Bechstein’s
393 bats (*Myotis bechsteinii*). *Behaviour* 136: 1187–1202.
394
- 395 Kerth G, Weissmann K, König B. 2001. Day roost selection in female Bechstein’s bats (*Myotis*
396 *bechsteinii*): a field experiment to determine the influence of roost temperature.
397 *Oecologia* 126: 1–9.
398
- 399 Kiser M, Kiser S. 2004. A decade of bat house discovery. Newsletter of the North American bat
400 house research project, *The bat house researcher* 12(4): 1-12. Available at
401 [https://www.batcon.org/pdfs/bat houses/ResearchFinal.pdf](https://www.batcon.org/pdfs/bat%20houses/ResearchFinal.pdf) (accessed 2 October 2018)
402
- 403 Kunz TH, Braun de Torrez, E, Bauer D, Lobova T, Fleming TH. 2011. Ecosystem services provided
404 by bats. *Annals of the New York Academy of Science* 1223:1-38.
405
- 406 Lewis SE. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* 76(2): 481-496.
407
- 408 Lopez-Hoffmann L, Wiederholt R, Sansone, C, Bagstad KJ, Cryan P, Jay E, Diffendorfer JE,
409 Goldstein J, Lasharr K, Loomis J, McCracken G, Medellin RA, Russel A, Semmens D. 2014. Market
410 Forces and Technological Substitutes Cause Fluctuations in the Value of Bat Pest-Control
411 Services for Cotton. *PLoS ONE* 9(2): e87912.
412
- 413 Lourenco SI. and Palmeirim JM. 2004. Influence of temperature in roost selection by *Pipistrellus*
414 *pygmaeus* (Chiroptera): relevance for the design of bat boxes. *Biological Conservation* 119:
415 237–243.
416
- 417 Maas B, Clough Y, Tscharrntke T. 2013. Bats and birds increase crop yield in tropical agroforestry
418 landscapes. *Ecology Letters* 16: 1480–1487.
419
- 420 Meteoblue, 2018. Climate Ratombo. Available at
421 [https://www.meteoblue.com/en/weather/forecast/modelclimate/ratombo_south-](https://www.meteoblue.com/en/weather/forecast/modelclimate/ratombo_south-africa_963100)
422 [africa_963100](https://www.meteoblue.com/en/weather/forecast/modelclimate/ratombo_south-africa_963100) (Accessed 15 December 2018)
423

- 424 McCracken GF, Westbrook, JK, Brown VA, Eldridge M, Federico P, Kunz TH.
425 2012. Bats track and exploit changes in insect pest populations. *PLoS One* 7(8): e43839.
426
- 427 Meddings A, Taylor S., Batty L, Green R, Knowles M, Latham D. 2011. Managing competition
428 between birds and bats for roost boxes in small woodlands, northeast England. *Conservation*
429 *Evidence* 8:74–80.
430
- 431 Mickleburgh SP, Hutson AM, Racey PA. 2002. A review of the global conservation status of
432 bats. *Oryx* 36:18–34.
433
- 434 Monadjem A, Raabe T, Dickerson B, Silvy N, McCleery R. 2010 (a). Roost use by two sympatric
435 species of *Scotophilus* in a natural environment. *South African Journal of Wildlife Research*
436 40(1):73-76.
437
- 438 Monadjem A, Taylor PJ, Cotterill FPD, Schoeman MC. 2010 (b). Bats of Southern and
439 Central Africa: A Biographic and Taxonomic Synthesis. Wits University Press, Johannesburg.
440
- 441 Monadjem A, Reside A, Cornut J, Perrin MR. 2009. Roost selection and home range of an
442 African insectivorous bat *Nycteris thebaica* (Chiroptera, Nycteridae). *Mammalia* 73: 353–359.
443
- 444 Natuschke G., 1960: Heimische Fledermäuse. Die Neue Brehm-Bücherei Nr. 269. Frankh'sche
445 Verlagsbuchhandlung. Stuttgart. [Not seen, cited after Schwenke, 1983].
446
- 447 Park KJ. 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential role
448 as bioindicators. *Mammalian Biology* 80:191-204.
449
- 450 Puig-Montserrat X, Torre I, López-Baucells A, Guerrieri E, Monti MM, Ràfols-García R, Ferrer
451 X, Gisbert D, Flaquer C. 2015. Pest control service provided by bats in Mediterranean rice
452 paddies: linking agroecosystems structure to ecological functions. *Mammalian Biology* 80(3):
453 237-245.
454
- 455 R Core Team, 2017. R: A Language and Environment for Statistical Computing. R
456 Foundation for Statistical Computing, Vienna, Austria (Available from). [https://](https://www.R-project.org/)
457 www.R-project.org/ (accessed 7 July 2017)
458
- 459 Rainho A, and Palmeirim JM. 2011. The importance of distance to resources in the spatial
460 modelling of bat foraging habitat. *PLoS One* 6(4):e19227.
461
- 462 Reckardt K, and Kerth G. 2006. The reproductive success of the parasitic bat fly *Basilisa nana*
463 (Diptera: Nycteribiidae) is affected by the low roost fidelity of its host, the Bechstein's bat
464 (*Myotis bechsteinii*). *Parasitology Research* 98(3): 237-243.
465
- 466 Ruegger N. 2016. Bat boxes—a review of their use and application, past, present and future.
467 *Acta Chiropterologica* 18(1):279-299.

- 468
469 Russo D, Ancillotto L. 2015. Sensitivity of bats to urbanization: a review. *Mammalian Biology*
470 80(3):205-212.
471
- 472 Sedgeley JA. 2001. Quality of cavity microclimate as a factor influencing selection of maternity
473 roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied*
474 *Ecology* 38(2):425-438.
475
- 476 Schwenke W. 1983. Zur Ansiedlung von Singvögeln und Fledermäusen in Kunsthöhlen in
477 Kieferwäldern, unter besonderer Berücksichtigung früherer und neuer Kontrollergebnisse im
478 Geisenfelder Forst, Oberbayern. *Anzeiger für Schädlingskunde. Pflanzenschutz, Umweltschutz*
479 5:52–58.
480
- 481 Shek C, So JWK, C., Lau TY, Chan CSM, Li AOY, Chow WSH, Liu CSK. 2012. Experimentation on
482 the use of bat boxes in Hong Kong. *Hong Kong Biodiversity* 22:10–15.
483
- 484 Smith GC, and Agnew G. 2002. The value of ‘bat boxes’ for attracting hollow-dependent fauna
485 to farm forestry plantations in southeast Queensland. *Ecological Management and*
486 *Restoration* 3:37–46.
487
- 488 Taylor PJ. 2000. Bats of Southern Africa. Guide to their Biology, Identification and
489 Conservation. University of Natal Press, Pietermaritzburg. 206 pp.
490
- 491 Taylor PJ, Monadjem, A., Steyn, J.N., 2013. Seasonal patterns of habitat use by insectivorous
492 bats in a subtropical African agro-ecosystem dominated by macadamia
493 orchards. *African Journal of Ecology* 51:552–561.
494
- 495 Taylor, P.J., Matamba E, Steyn JN, Nangammbi T, Zepeda-Mendoza ML, Bohmann K. 2017. Diet
496 determined by next generation sequencing reveals pest consumption and opportunistic
497 foraging by bats in macadamia orchards in South Africa. *Acta Chiropterologica* 19:239–254.
498 <https://doi.org/10.3161/15081109ACC2017.19.2.003>.
499
- 500 Taylor PJ, Grass I, Alberts AJ, Joubert E, Tschardt T. 2018. Economic value of bat predation
501 services – A review and new estimates from macadamia orchards. *Ecosystem Services* 30:372-
502 381.
503
- 504 Tilman D, Fargione J, Wolff B, D’Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH,
505 Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental
506 change. *Science* 292:281–284.
507
- 508 Tschardt T, Clough Y, Wanger TC, Jackson L, Motzke I, Perfecto I, Vandermeer J, Whitbread
509 A. 2012. Global food security, biodiversity conservation and the future of agricultural
510 intensification. *Biological conservation* 151(1): 53-59.
511

- 512 Tuttle MD, Kiser M, Kiser S. 2013. The bat house builder's handbook. University of Texas Press.
513 Available at <http://www.batcon.org/pdfs/BatHouseBuildersHandbook.pdf> (accessed 5 May
514 2015)
515
- 516 Voigt C. and Kingston T. 2016. Bats in the Anthropocene: Conservation of Bats in a Changing
517 World, Springer International Publishing, Switzerland.
518
- 519 Wanger TC, Darras K, Bumrungsri S, Tschardtke T, Klein AM. 2014. Bat pest control contributes
520 to food security in Thailand. *Biological Conservation* 171:220-223.
521
- 522 Weier S. M., Grass I, Linden VMG, Tschardtke T, Taylor PJ. 2018. Natural vegetation and bug
523 abundance promote insectivorous bat activity in macadamia orchards, South Africa. *Biological
524 Conservation* 226:16-23.

Table 1 (on next page)

Final model testing the relationship between the occupancy of bathhouses and the different types of bathhouses in macadamia orchards, Levubu, South Africa (significance level of bold $p < 0.05$).

1

Variable	Estimate	SE	Z	p-Value	AICc
Null model					388.2
Type of bathouse					364.6
6-Chamber	1.43	0.41	3.45	0.000	
Black	2.30	0.56	4.08	0.000	
Nursery box	0.50	0.45	1.10	0.268	
Rocket box	-0.50	0.62	-0.81	0.415	
White	0.57	0.67	0.85	0.394	

2

3

4

Figure 1

Map showing the aerial image of the study area with the location of the different bat houses and the study area in Levubu, Limpopo, South Africa (Google Maps 2018; QGIS version 2.18.11).

A) Study area with the location of each bat house B) showing a detailed example of one study site and C) the location of the study area (white circle) in Levubu, Limpopo, South Africa.

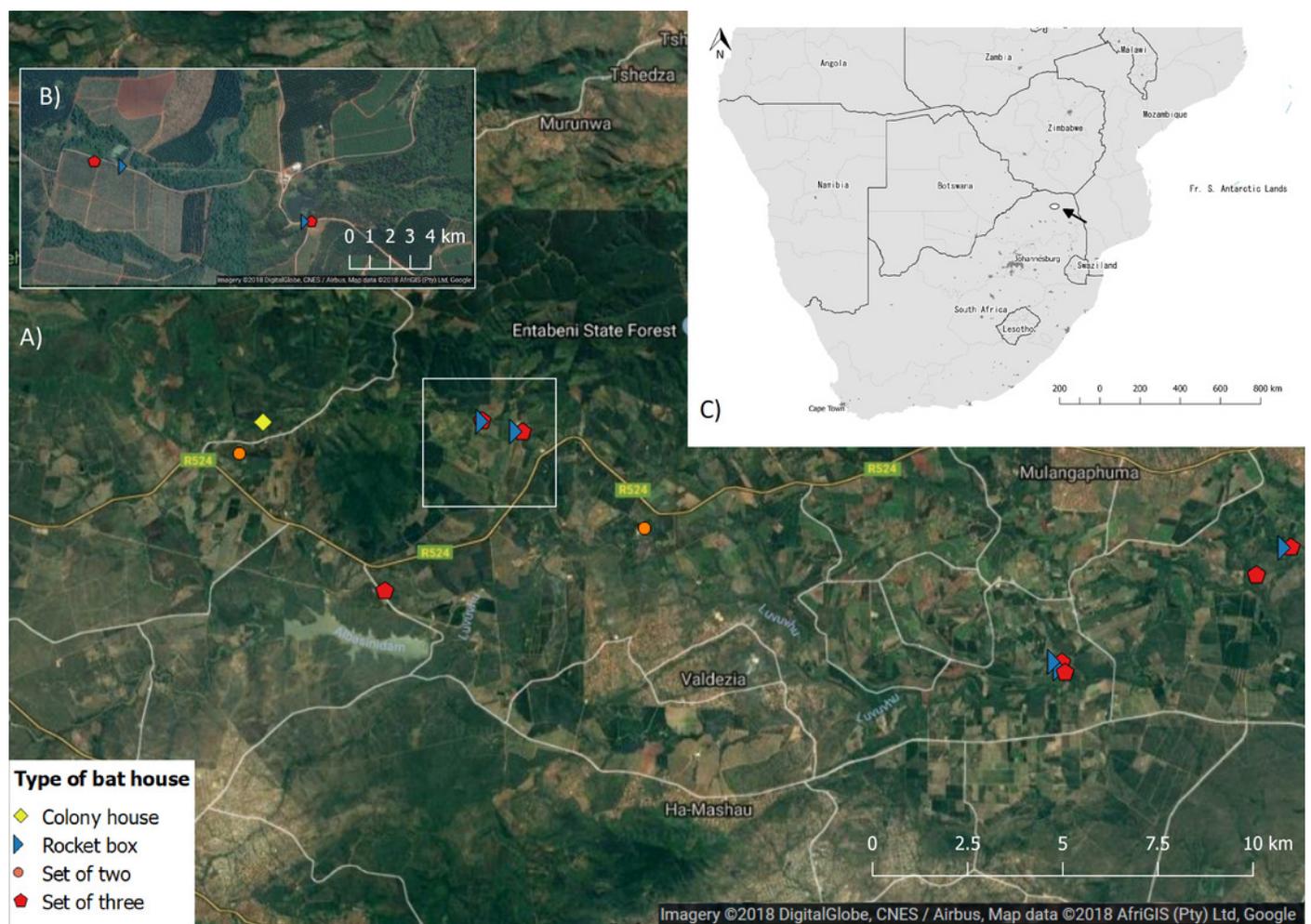


Figure 2

Showing the different bat house designs from the front and below, erected in the study area Levubu, Limpopo, South Africa. Photo credit: S.M. Weier

A) showing the set of three houses B) showing the set of black and white bat houses C) showing the Rocket box design and D) showing the Colony bat house. The below view showing E) the Old George, the 6-Chamber and the Nursery bat house (left to right) F) black and white house G) Rocket box H) Colony bat house.

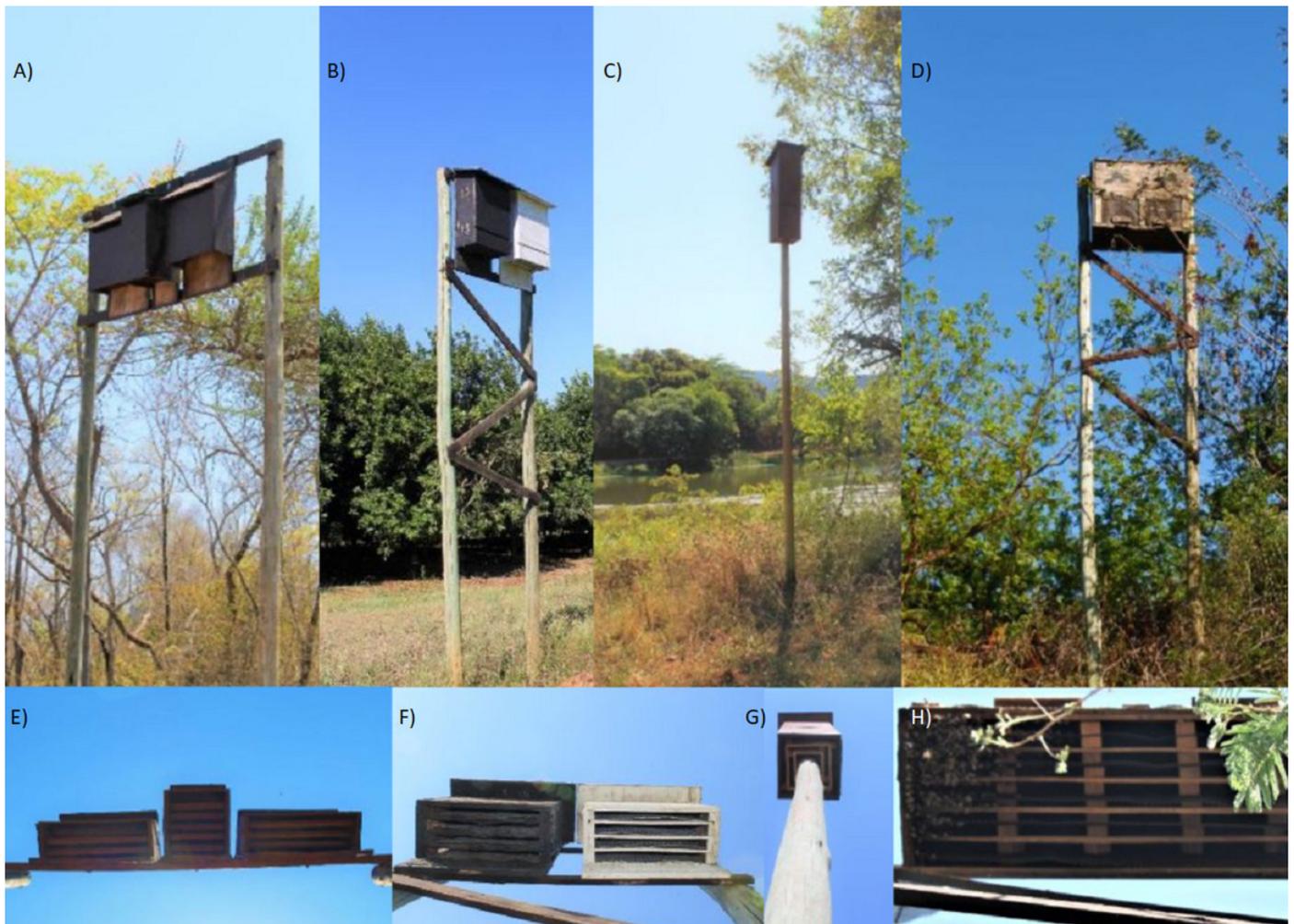


Figure 3(on next page)

Figure 3 Showing the probability (Confidence intervals of 95%) of a certain type of bat house being occupied with in the study area Levubu, Limpopo, South Africa.

Bat house A (=Old George), bat house B (=6-Chamber) and bat house C (=Nursery) are always set up in sets of three with the 6-Chamber bat house in the middle. The black and white painted bat houses are also erected in sets. Annotated letters show same probability of occupancy (same letter) or a significant difference in occupancy levels (different letter).

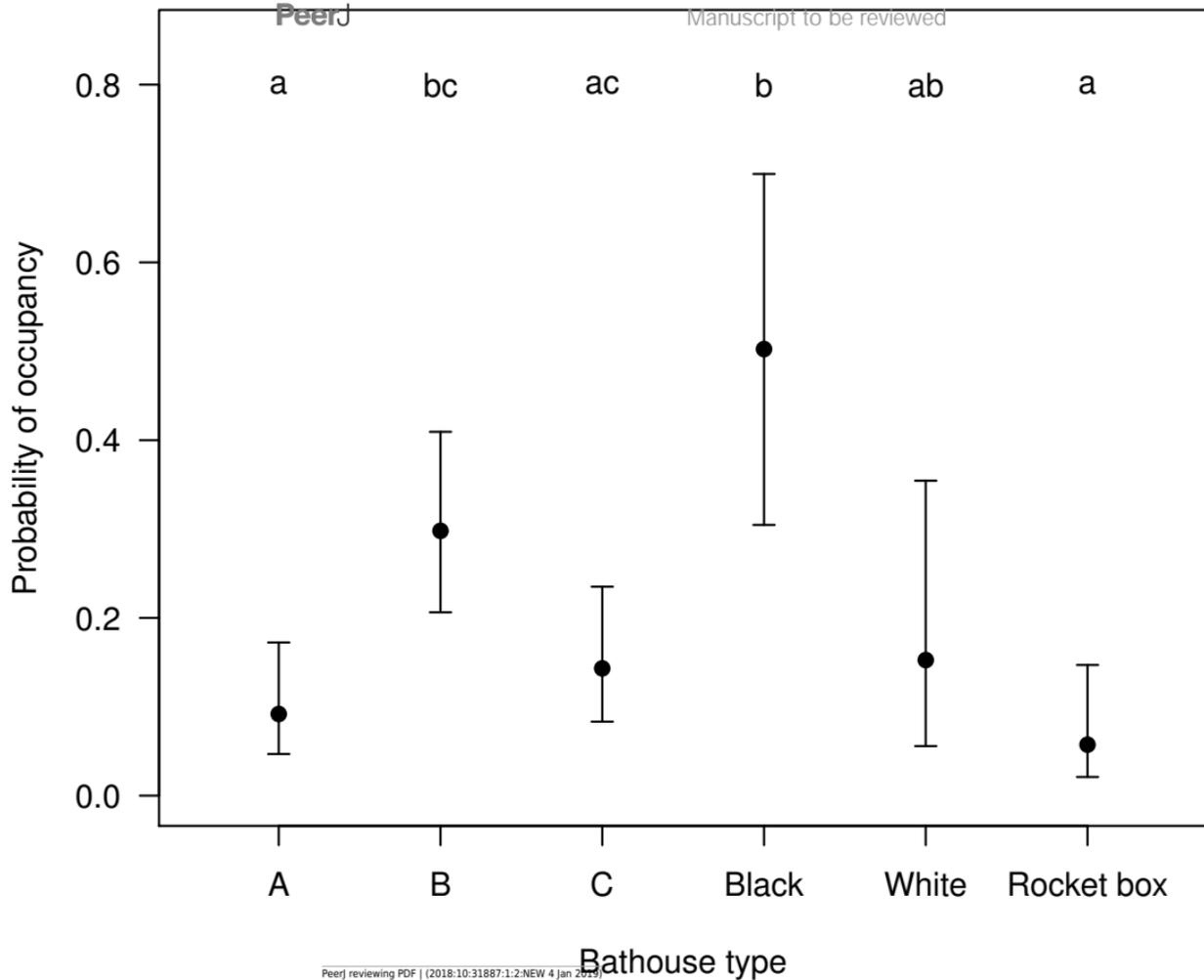


Figure 4

A Common Slit-faced Bat (*Nycteris thebaica*) foraging on a green vegetable stinkbug (*Nezara viridula*) in the study area Levubu, Limpopo, South Africa. Photo credit: ©MerlinTuttle.org

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

