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1 Movements and use of space by Mangrove Cuckoos (*Coccyzus minor*) in Florida, USA

2

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10

11 Abstract

12 I used radio-telemetry to track the movements of Mangrove Cuckoos (*Coccyzus minor*) captured
13 in southwest Florida. Relatively little is known about the natural history of Mangrove Cuckoos,
14 and my goal was to provide an initial description of how individuals use space, with a focus on
15 the size and placement of home ranges. I captured and affixed VHF radio-transmitters to 32
16 individuals between 2012 and 2015, and obtained a sufficient number of relocations from 16 of
17 them to estimate home-range boundaries and describe patterns of movement. Home-range area
18 varied widely among individuals, but in general, was roughly four times larger than expected
19 based on the body size of Mangrove Cuckoos. The median core area (50% isopleth) of a home
20 range was 42 ha (range: 9 – 91 ha), and the median overall home range (90% isopleth) was 128
21 ha (range: 28 – 319 ha). The median distance between estimated locations recorded on
22 subsequent days was 298 m (95% CI = 187 m – 409 m), but variation within and among
23 individuals was substantial, and it was not uncommon to relocate individuals >1 km from their
24 location on the previous day. Site fidelity by individual birds was low; although Mangrove
25 Cuckoos were present year-round within the study area, I did not observe any individuals that
26 remained on a single home range throughout the year. Although individual birds showed no
27 evidence of avoiding anthropogenic edges, they did not incorporate developed areas into their
28 daily movements and home ranges consisted almost entirely of mangrove forest. The persistence
29 of the species in the study area depended on a network of conserved lands – mostly public, but
30 some privately conserved land as well – because large patches of mangrove forest did not occur
31 on tracts left unprotected from development.

32

33 Introduction

34 Understanding how animals use space and move through the environment around them can
35 provide important insights into their ecology and conservation (Kramer and Chapman, 1999;
36 Wiens, 2008; Holland et al., 2009). Information concerning an animal's home range - that is, the
37 area in which an organism carries out the day-to-day activities of life (Burt, 1943) - can be
38 particularly useful, helping to identify habitat requirements, predict sensitivity to habitat loss and
39 fragmentation, and delineate areas important for conservation. In this study, I documented
40 patterns of movement and described the characteristics of Mangrove Cuckoo (*Coccyzus minor*
41 Gmelin) home ranges in southwest Florida, USA. Mangrove Cuckoos are widespread and
42 relatively common in a variety of forested environments throughout the Caribbean and Middle
43 America (Lloyd, 2013). In Florida, the northern limit of their geographic distribution, they are
44 uncommon and apparently restricted largely to mangrove forests (Lloyd, 2013; Lloyd and Slater,
45 2014). Although the species is of Least Concern globally (BirdLife International, 2012),
46 Mangrove Cuckoos in the United States are a high priority for conservation action (Partners in
47 Flight Science Committee, 2012) and are considered at risk of becoming threatened (U.S. Fish
48 and Wildlife Service, 2008), with some evidence of recent declines in parts of Florida (Lloyd and
49 Doyle, 2011). An important obstacle to planning conservation action, however, is the lack of
50 information on the natural history of Mangrove Cuckoos; they remain one of North America's
51 least-studied birds (Hughes, 2010).

52

3

53 The goal of this study was to enhance understanding of the natural history of Mangrove Cuckoos
54 by providing an initial description of space use; as with other facets of the species' ecology, basic
55 patterns of space use are undocumented. To address this information gap, I sought to quantify
56 patterns of movement among individuals, estimate the amount of area required to support a
57 Mangrove Cuckoo home range, and describe qualitatively the land-cover types in which
58 Mangrove Cuckoos will establish a home range. Information on area requirements and habitat
59 use may help inform future conservation planning efforts. I did not document what sorts of
60 activities birds engaged in during the period of time that I followed them (e.g., whether they
61 were nesting), so here I adopt a simple empirical approach of allowing the movement of
62 individual birds to define an area of concentrated use that I refer to as a home range (sensu Burt,
63 1943).

64

65 Methods

66 Study area

67 I captured Mangrove Cuckoos from 2012-2015 at J.N. “Ding” Darling National Wildlife Refuge
68 (26.44°N, -82.11°W)(hereafter, “Ding Darling NWR”) on the barrier island of Sanibel and at San
69 Carlos Bay – Bunche Beach Preserve (26.48°N, -81.97°W) on the nearby mainland coast in Fort
70 Myers. The study area, however, encompassed all of the locations where I relocated marked
71 birds, ranging from near Port Charlotte to Fort Myers Beach (Fig. 1). Mangrove forests fringe
72 protected coastlines in this area and are dominated by red (*Rhizophora mangle* L.) and black
73 (*Avicennia germinans* L.) mangrove, with lesser numbers of white mangrove (*Laguncularia*

74 *racemosa* C. F. Gaertn.). The inland edge of most mangrove forest in the region abuts developed
75 land, because nearly all uplands have been cleared of native vegetation for commercial and
76 residential development. Where uplands have been protected - almost exclusively on Sanibel -
77 adjacent forest types include hammock forests dominated by southern live oak (*Quercus*
78 *virginiana* Mill.) and a variety of tropical hardwoods, savannas of cabbage palm (*Sabal palmetto*
79 Lodd. ex Schult.f.), and pure stands of buttonwood (*Conocarpus erectus* L.) (Cooley, 1955).

80

81 The climate of the area is tropical (Duever et al., 1994). Air temperatures remain relatively warm
82 throughout the year, with mean monthly temperature ranging from 17.8°C in January to 28.1°C
83 in August (based on climate data from 1892-2012 collected in Fort Myers; available online at
84 <http://www.sercc.com>). Frosts are uncommon, especially in mangroves. Most (65%) of the mean
85 annual precipitation (136 cm) falls during convective storms in the pronounced wet season (June
86 to September). Weather between October and May is drier and cooler, and precipitation that falls
87 during the dry season is generally driven by the passage of cold fronts. Tropical cyclones strike
88 occasionally, although none affected the area during this study.

89

90 Field methods

91 I located birds by broadcasting recorded vocalizations of Mangrove Cuckoo, to which
92 individuals respond readily when present (Frieze et al., 2012), in areas of suitable habitat
93 (mangrove forest) that could be accessed by boat, on foot, or by motor vehicle. In 2012, searches
94 were conducted between March and August; in 2013, between February and August; and then

95 continually from February 2014 - June 2015.

96 Once a bird had been located, it was lured into a mist net via playback of recorded vocalizations.

97 Upon capture, each bird was marked with an aluminum US Fish and Wildlife Service leg-band

98 and a unique combination of three colored plastic leg-bands. A VHF radio-transmitter (American

99 Wildlife Enterprises, Monticello, Florida and ATS, Isanti, Minnesota) was attached using flat,

100 2.5-mm-wide elastic fabric to create leg loops as per Rappole and Tipton (1991). The transmitter

101 and harness collectively weighed 1.8 g, or approximately 2.9% of the average mass of Mangrove

102 Cuckoos captured in this study (mean body mass = 62.5 g; n = 46). Protocols and materials used

103 in capture, handling, and marking were designed in accordance with guidelines presented by Fair

104 et al. (2010). This research was conducted with the permission of the US Fish and Wildlife

105 Service (Special Use Permit No.13036), the USGS Bird Banding Laboratory (Bird-Banding

106 Permit No. 23726 issued to JDL), and the State of Florida (Scientific Collecting Permit No.

107 LSSC-11-00048A).

108

109 Birds were released as soon as possible after capture (average time between capture in the mist

110 net and release of a radio-marked bird was 27 minutes). I attempted to relocate radio-marked

111 birds every 1-3 days using a handheld antenna, although this frequency of relocation was

112 possible only for birds that remained in the core of the study area. Individuals that moved long

113 distances or occupied remote areas that could only be searched by plane were relocated less

114 frequently, generally every 2-3 weeks.

115

116 When an individual could not be located after multiple ground-based searches, a fixed-wing
117 airplane was used to search a wider area. Aerial searches typically focused on an area within 60
118 km of the last known location. Location of individuals detected during aerial searches was
119 estimated from the plane's Global Positioning System (GPS) after the signal had been localized
120 using directional antennae and close circling by the pilot.

121

122 Radio-marked individuals were tracked throughout each field season (see above for dates) or
123 until multiple aerial searches failed to detect them. The nominal battery life of the transmitters
124 ranged from 3-6 months depending on the unit, but in general I could not distinguish battery
125 failure from permanent emigration out of the search area.

126

127 Estimating telemetry error

128 To test the telemetry system, a naïve observer used biangulation to identify the location of a
129 radio transmitter that had been placed in a known location by a second observer. The transmitters
130 were placed on horizontal limbs of mangrove trees in locations that were representative of
131 perches used by Mangrove Cuckoos. I conducted 16 trials; 6 in February of 2012 and 10 in July
132 of 2012. The same observer was used in every trial. In 14 trials, the observer was able to obtain
133 bearings from land, but in the other 2 trials the location of the hidden transmitter required the
134 observer to take bearings from a kayak. I calculated error as the distance between the actual
135 location of the transmitter as determined by a handheld GPS unit and the location estimated from
136 biangulation.

137

138 Efficacy of aerial searches

139 I also conducted a test of the efficacy of aerial searches from a fixed-wing airplane. On a single
140 day, a pilot flew at different altitudes above a transmitter positioned at a known location in a
141 mangrove forest. The plane passed directly over the transmitter at 305 m, 457 m, and 610 m, and
142 then flew passes at different distances to either side of the transmitter, again repeating passes at
143 each of the 3 altitudes.

144

145 Statistical analysis of movements and space use

146 I estimated the location of marked birds by triangulating the signal based on compass bearings
147 and GPS locations obtained in the field. I described home ranges of radio-marked Mangrove
148 Cuckoos using the Brownian bridges movement model of Horne et al. (2007), as implemented in
149 the R package adehabitatHR (Calenge, 2006). This model requires time-stamped locations and
150 two smoothing parameters, one related to the speed at which the organism moves through space
151 (the Brownian motion variance parameter) and one that describes the imprecision of estimated
152 locations. I calculated the Brownian motion variance parameter using the likelihood method
153 proposed by Horne et al. (2007) and implemented by the liker function in the adehabitatHR
154 package. I used the results of the ground-based telemetry-error tests to calculate the standard
155 deviation of the mean location error, the second smoothing parameter (I have only qualitative
156 information about error during aerial searches). In estimating the boundaries of home ranges, I
157 censored from analysis any individuals with ≤ 20 relocations due to concerns about small-sample

158 bias. Based on the recommendation of Borger et al. (2006), I defined the total home range as the
159 90% isopleth of the utilization distribution, and the core home range as the 50% isopleth.

160 Location data used to estimate the home-range boundaries are available in Lloyd (2017).

161

162 Home-range boundaries for Mangrove Cuckoos in this area tended to include large areas of open
163 water, which I did not include in calculations of home-range area. The amount of open water
164 within each home range was calculated using a shapefile of the Florida coastline (version 2004)
165 published by the State of Florida (available at <http://www.fgdl.org>) and then subtracted from the
166 area within the 90% and 50% isopleths. Home-range size calculations were performed within
167 QGIS version 2.16.3 (QGIS Development Team 2016); all other analyses were conducted in R
168 3.2.4 (R Core Team 2016).

169

170 I used the shapefile (version April 2015) published by the Fish and Wildlife Research Institute
171 (FWRI) at the Florida Fish and Wildlife Conservation Commission to determine the distribution
172 of mangrove vegetation within the study area (available at <http://www.fgdl.org>). I determined
173 protected area boundaries using version 1.4 of the U.S. Geological Survey's Protected Areas
174 Database of the United States (available at: <http://gapanalysis.usgs.gov/padus/>).

175

176 Results

177 Telemetry error

178 The estimated mean telemetry error associated with ground-based searches was 35.1 m (SD =

179 28.6 m; range = 5.7 m - 105.3 m).

180 Efficacy of aerial searches

181 Flying directly over the transmitter at 305 m altitude, the signal was detected 1.1 km before the
182 plane passed over the transmitter and was lost when the plane had passed 1.0 km beyond the
183 location of the signal. At this altitude, the signal was not detected at the 1 or 2 km offset passes.
184 At 457 m altitude, the signal was detected 1.8 km before the plane passed over the transmitter
185 and was lost when the plane had passed 800 m beyond the transmitter. The signal was located on
186 offset passes as far as 2 km adjacent to the path directly over the signal. At 610 m altitude, the
187 signal was detected 1.7 km before the plane passed over the transmitter and was lost when the
188 plane had passed 900 m beyond the transmitter. The signal was located on offset passes as far as
189 2 km adjacent to the path directly over the signal. These results suggest that, at altitudes typical
190 of those maintained during aerial searches (> 400 m), the detection radius for a transmitter on the
191 ground was approximately 1-2 km. By comparison, patches of mangrove forests in the study area
192 were always <4 km in width, and most were <1 km wide (e.g., Fig. 1).

193

194 Movements and space use by Mangrove Cuckoos

195 I captured 46 individuals between 2012 and 2015. I did not recapture or resight any marked
196 individuals outside of the year in which they were initially captured (except for one individual
197 captured in late 2014 and tracked into early 2015). I captured individuals in every month except
198 February, but most captures ($n = 27$) occurred between March and May (Fig. 2). I radio-marked
199 32 of these individuals, and obtained an adequate number of relocations for 16 of these to

200 describe a home range. Of the 16 individuals censored from the home-range analysis due to
201 small sample size, six were tracked for relatively long periods of time (127,123,114,111, 103,
202 and 45 days, respectively) but occupied areas where transmitter signals could only be detected by
203 plane and thus were relocated infrequently. The other 10 were transient (or carried transmitters
204 that failed prematurely); most of these individuals were known to be present in the study area for
205 < 2 weeks (average number of days known present = 13; range = 2-31 days).

206

207 In general, individuals moved widely from day to day. The median distance between estimated
208 locations recorded on subsequent days was 298 m (95% CI = 187 m – 409 m), but variation
209 within and among individuals was substantial, and it was not uncommon to relocate individuals
210 >1 km from their location on the previous day (Fig. 3). Notable movements included a flight
211 taken by individual 150.919 from its home range in Ding Darling NWR to the San Carlos Bay –
212 Bunche Beach Preserve and back again, a round-trip distance of roughly 35 km. This individual
213 was located on its home range at 07:01 on 18 July 2012, but by the following morning at 09:59 it
214 had moved to a location in San Carlos Bay – Bunche Beach Preserve on the mainland, a straight-
215 line distance of 16.8 km. It was not located on 20 July. On 21 July at 08:06 it had returned to
216 nearly the same location where it had been found on 18 July. This individual then remained on
217 its home range on Sanibel until at least 21 November 2012, and during that time made no other
218 similar movements. Although the purpose of that single long-distance movement is unknown, it
219 was evidently not part of a dispersal event to a new home range.

220

221 Home-range area was generally large but variable among individuals (Table 1). Home-range area
222 did not covary with the length of the period during which I tracked each individual (total home
223 range: $r = 0.30$, 95% CI = $-0.23 - 0.69$; core area: $r = 0.26$, 95% CI = $-0.25 - 0.66$) or with the
224 number of times an individual was relocated (total home range: $r = 0.29$, 95% CI = $-0.24 - 0.69$;
225 core area: $r = 0.16$, 95% CI = $-0.35 - 0.59$). Of the 16 individuals for which I estimated a home
226 range, 11 were last detected within its boundaries. The other 5 individuals (150.613, 150.757,
227 149.881, 148.872, and 149.281) were later located 1-3 times at locations far removed from the
228 home-range boundaries (c.a. 12-55 km from the last estimated location within the home range).
229 None of these five individuals ever returned, and thus presumably had abandoned the home
230 range and were in the process of dispersing when last located. Timing of departure, for these five
231 individuals, ranged from early May (149.281) to late July (150.757). The trigger for these
232 dispersal events is unknown.

233

234 The same areas were frequently used as home ranges by different birds in different years, but
235 concurrent use of overlapping home ranges or core-use areas was observed in only one instance.
236 Three individuals – 150.775, 150.829, and 150.819 – occupied broadly overlapping (i.e., >50%
237 overlap) home ranges and core-use areas at the same time in San Carlos Bay – Bunche Beach
238 Preserve. I did not observe interactions among these individuals, so it is unclear whether they
239 were part of a social unit. However, all three individuals were located in close proximity to one
240 another on numerous occasions throughout the period during which they were tracked.

241

242 Nearly 75% of estimated locations of marked Mangrove Cuckoos fell within areas classified as
243 mangroves (756 locations from a total of 1,015 locations gathered during the course of the study)
244 and 94% of all estimated locations fell within 100 m of mangrove vegetation as defined by the
245 FWRI shapefile. Mangrove vegetation in the study area is limited primarily to protected areas,
246 and as consequence nearly every (99%; n = 1002 locations) estimated location of a Mangrove
247 Cuckoo occurred within a protected area. In addition to the two main capture areas, Ding Darling
248 NWR (n = 590 locations) and San Carlos Bay – Bunche Beach Preserve (n = 156 locations),
249 other protected areas used by Mangrove Cuckoos included conservation lands managed by
250 Sanibel-Captiva Conservation Foundation (n = 68), Charlotte Harbor Preserve State Park (n =
251 35), Estero Bay Preserve State Park (n = 22), and Matlacha Pass NWR (n = 6).

252

253 Discussion

254 Home-range size of Mangrove Cuckoos in southwest Florida was substantially larger than
255 predicted based on the allometry of space use by animals (Schoener, 1968; Mace and Harvey,
256 1983). Indeed, with a median home-range size of 132 ha, space use by Mangrove Cuckoos is
257 similar to that of a small raptor such as Red-shouldered Hawk (*Buteo lineatus* Gmelin; average
258 home-range size = 135 ha) (Peery, 2000), even though its body size is roughly 15% that of the
259 Red-shouldered Hawk. Little information exists on home-range size of other New World
260 cuckoos. Yellow-billed Cuckoos (*Coccyzus americanus* Linnaeus) in riparian forests in Arizona
261 occupied home ranges that averaged 39 ha (95% kernel-density estimate) to 51 ha (minimum
262 convex polygon) during the breeding season (Haltermann, 2009), and a single Banded Ground-

263 cuckoo (*Neomorphus radiolosus* Sclater & Salvin) – a distantly related and far larger species –
264 occupied a home-range in Ecuador estimated to consist of 42.2 ha (MCP) to 49.9 ha (95%
265 kernel-density estimate) (Karubian and Carrasco, 2008). Likewise, information on space use by
266 other birds of mangrove forest is scarce; Yellow-billed Cotinga (*Carpodectes antoniae*
267 Ridgway), a substantially larger (85-90g) inhabitant of mangrove forests in Costa Rica and
268 Panama, used somewhat smaller home ranges (31.2 ha and 107.2 ha, respectively, during the
269 breeding and non-breeding seasons) and core-use areas (6.6 ha and 24.3 ha, respectively)
270 (Leavelle et al., 2015).

271

272 The Mangrove Cuckoos tracked in this study showed no inter-annual site fidelity. I documented
273 several instances in which the same patch of mangrove was occupied by a different individual in
274 each year of the study. Indeed, during the course of the study, I never recaptured – and only once
275 resighted – an individual marked in a previous year; this suggests a nomadic lifestyle, as has
276 been argued for other *Coccyzus* cuckoos. Although Mangrove Cuckoos were present in the study
277 area year-round, I found no evidence that any individual remained resident in the same area
278 throughout the year.

279

280 Why might Mangrove Cuckoos use disproportionately large home ranges and show an apparent
281 tendency to wander widely? Perhaps it is worth considering use of space within the context of
282 the unusual suite of life-history traits that seem to characterize Mangrove Cuckoo and two of its
283 more well-studied congeners: Yellow-billed Cuckoo and Black-billed Cuckoo (*C.*

284 *erythroptalmus* Wilson). Based on what is known of these species, in addition to occupying
285 large home ranges, they exhibit remarkably rapid developmental rates, are facultative
286 intraspecific brood parasites, have low inter-annual fidelity to breeding sites and highly variable
287 investment in reproduction, and seem to engage in inexplicable, long-distance movements before
288 and after breeding (Fleischer et al., 1985; Hughes, 2001, 2010, 2015; Dearborn et al., 2009;
289 Sechrist et al., 2012). These traits have been explained as an adaptation to a lifestyle centered
290 around exploiting super-abundant but patchy, ephemeral, and unpredictable food resources
291 (Hamilton and Hamilton, 1965; Nolan and Thompson, 1975; Sealy, 1985; Barber et al., 2008).
292 Evidence for this hypothesis is largely circumstantial, however (e.g., see Hughes, 1997 for a
293 critique), and it is not clear if the food resources used by Mangrove Cuckoos are as variable as
294 those considered critical for Yellow-billed and Black-billed cuckoos. The diet of Mangrove
295 Cuckoos is known poorly but seems to include a predilection for large invertebrates and small
296 vertebrates (Lloyd, 2013) and thus the large home ranges that I observed may have reflected a
297 diet focused on relatively large prey items – a characteristic associated with large home ranges
298 (Schoener, 1968) – rather than a diet based on highly variable prey populations. However, as
299 with other *Coccyzus* cuckoos, rigorous tests of these ideas await longer-term studies of breeding
300 biology and natural history. For Mangrove Cuckoos, this would include research that links
301 movement patterns to breeding behavior; tracks individuals across longer temporal and larger
302 spatial scales; and rigorously quantifies diets of adults, juveniles, and nestlings.

303

304 Although many puzzles remain concerning the natural history of Mangrove Cuckoos, the

305 conditions needed to conserve the species are clear: a network of intact, protected patches of
306 mangrove forest. In south Florida, this network consists almost entirely of publically owned land.
307 Stands of mangrove forest large enough to support Mangrove Cuckoos do not occur on private
308 land. Some important protected areas – Ding Darling NWR, for example – were established to
309 conserve habitat for wildlife, but other important protected areas, like Charlotte Harbor Preserve
310 State Park, were established largely for shoreline protection and water-quality improvement. No
311 matter what the rationale for investing in mangrove protection, the continued persistence of
312 Mangrove Cuckoos in Florida depends on the preservation of remaining mangrove forests.

313 Animal Ethics

314 All research activities were conducted in accordance with the Guidelines to the Use of Wild
315 Birds in Research (Fair et al. 2010).

316

317 Field Study Permissions

318 This research was conducted with the permission of the US Fish and Wildlife Service (Special
319 Use Permit No.13036), the USGS Bird Banding Laboratory (Bird-Banding Permit No. 23726
320 issued to JDL), and the State of Florida (Scientific Collecting Permit No. LSSC-11-00048A).

321

322 Data Deposition

323 All data used in this analysis are available at <https://doi.org/10.6084/m9.figshare.4628017.v1>

324

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334

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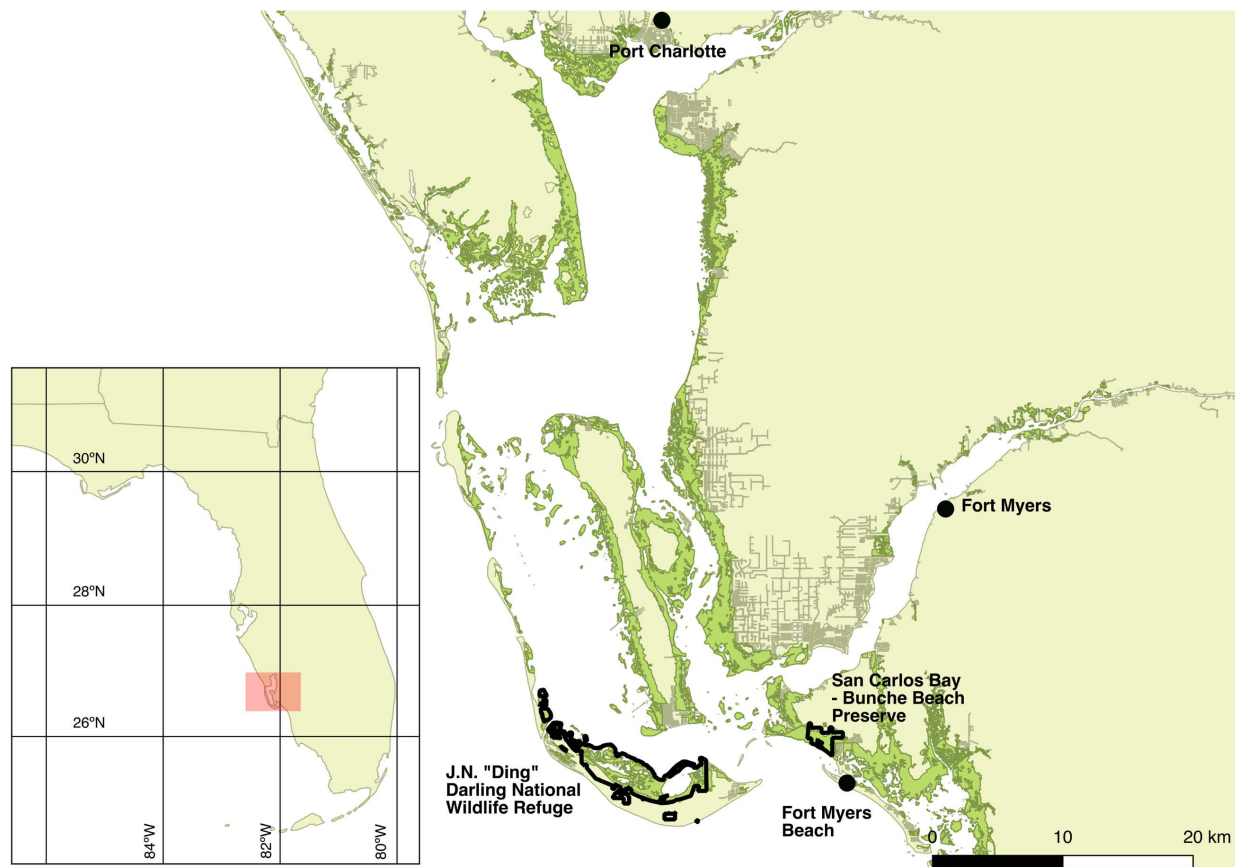
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458 Figure 1. Study area (red shaded box on the inset map) in southwest Florida, USA, where

459 Mangrove Cuckoos (*Coccyzus minor*) were radio-tracked during 2012-2015. Individuals were

460 captured in mangrove forest (green shading) within two protected areas: J.N. “Ding” Darling

461

462 National Wildlife Refuge, located on the barrier island of Sanibel, and San Carlos Bay – Bunche
463 Beach Preserve, located on the mainland in the city of Fort Myers. Individuals were tracked as
464 far north as Port Charlotte, and as far south as Fort Myers Beach.
465

466

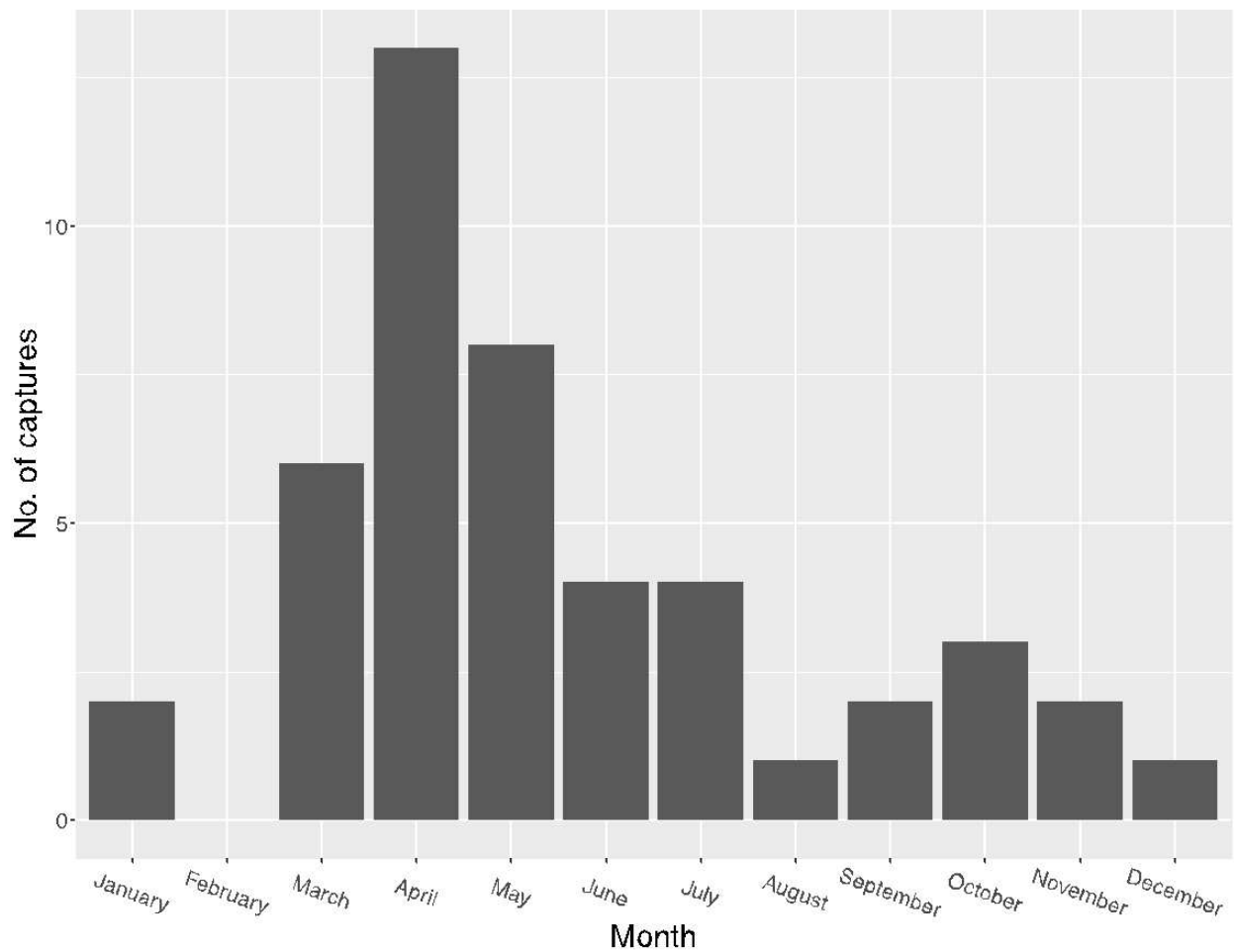
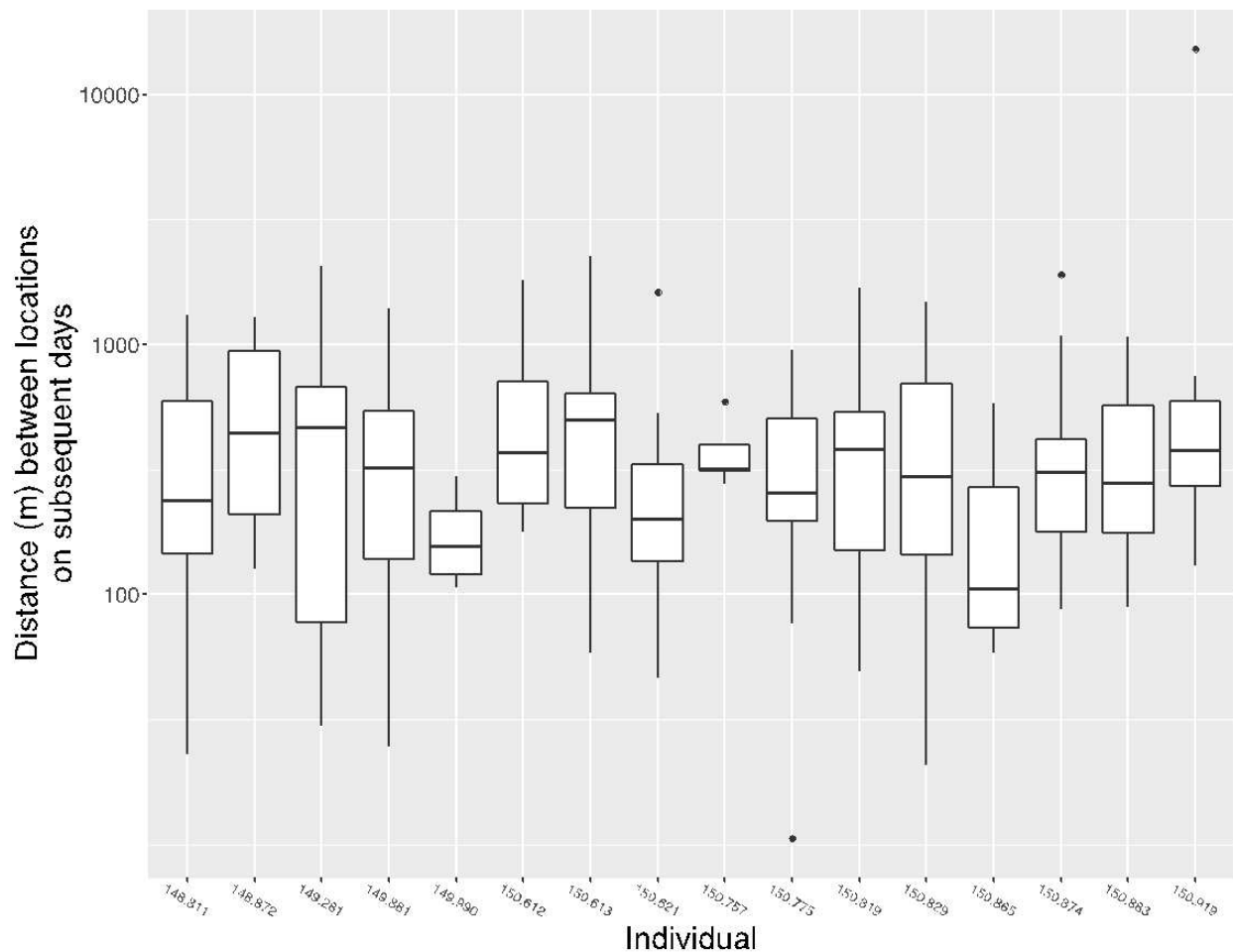
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Figure 2. Seasonal distribution of captures of Mangrove Cuckoos (*Coccyzus minor*) (n = 46) in southwest Florida during 2012-2015.

472



473

474 Figure 3. Distance between estimated locations of individual radio-tagged Mangrove Cuckoos

475 (*Coccyzus minor*) on subsequent days (i.e., estimated locations taken 18-28 hours apart) in

476 southwest Florida from 2012-2015. Only individuals (n = 16) with an adequate number of

477 relocations to estimate home-range boundaries are included.

478 Table 1. Home-range characteristics of 16 Mangrove Cuckoos (*Coccyzus minor*) tracked via
 479 radio-telemetry on the southwest coast of Florida from 2012-2015.
 480

Individual	N	Home-range area (ha)		Tracking dates
		Core area ^a	Total ^b	
148.811	57	42	153	3 Mar – 12 Jun 2014
148.872	39	79	243	11 Mar – 27 May 2014
149.281	20	91	243	4 Apr – 6 May 2014
149.881	47	70	294	18 Apr – 27 Jun 2014
149.990	26	9	28	25 Nov 2014 – 18 Jan 2015
150.612	37	24	92	28 Apr – 16 Jun 2012
150.613	53	15	104	7 Jun – 22 Aug 2013
150.621	42	30	107	8 May – 4 July 2012
150.757	31	64	NA	9 May – 30 Jul 2013
150.775	70	28	125	14 May – 22 Aug 2013
150.819	42	60	201	18 Jun – 22 Aug 2013
150.829	36	42	132	9 Jul – 22 Aug 2013
150.865	58	9	36	20 May – 22 Aug 2013
150.874	76	76	319	15 Mar – 15 Jul 2013
150.883	91	65	164	16 Mar – 22 Aug 2013
150.919	20	24	86	8 Jul – 10 Aug 2012
MEAN		45.5	155.1	
		(SD = 26.8)	(SD = 88.3)	
MEDIAN		42	132	

481 ^a50% isopleth from a Brownian bridges analysis.

482 ^b90% isopleth from a Brownian bridges analysis.