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Diverse habitat use during two life stages of the critically Endangered Bahama Oriole (*Icterus northropi*): Community structure, foraging, and social interactions

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Our ability to prevent extinction in declining populations often depends on effective management of habitats that are disturbed through wildfire, logging, agriculture, or development. In these disturbed landscapes, the juxtaposition of multiple habitat types can be especially important to fledglings and young birds, which may leave breeding grounds in human-altered habitat for different habitats nearby that provide increased foraging opportunities, reduced competition, and higher protection from predators. In this study, we sought to better understand the importance of habitat diversity to two life stages of the critically endangered Bahama Oriole (*Icterus northropi*), a synanthropic songbird endemic to Andros, The Bahamas. First, we determined the avian species composition and relative abundance of the oriole among three major vegetation types on Andros: Caribbean pine (*Pinus caribaea*) forest, coppice (broadleaf dry forest), and anthropogenic areas, dominated by nonnative vegetation (farmland and developed land). We then compared the foraging strategies and social interactions of two age classes of adult orioles in relation to differential habitat use. Bird surveys late in the oriole's breeding season indicated avian species richness and oriole density were highest in coppice. Some bird species occurring in the coppice and pine forest were never observed in agricultural or residential areas, and may be at risk if human disturbance of pine forest and coppice increases, as is occurring at a rapid pace on Andros. During the breeding season, second-year (SY) adult orioles foraged in all vegetation types, whereas after-second-year (ASY) adults were observed foraging only in anthropogenic areas, where the species nested largely in introduced coconut palms (*Cocos nucifera*). Additionally, SY adults foraging in anthropogenic areas were often observed with an ASY adult, suggesting divergent habitat use for younger, unpaired birds. Other aspects of foraging (vegetation features, food-gleaning behavior, and food items) were similar for the two age classes. Older orioles exhibited relatively higher rates of social interactions (intraspecific and interspecific

pooled) in anthropogenic areas, and won more interaction outcomes compared to younger adults. Our findings concur with those of other studies indicating dry broadleaf forest is vitally important to migrating, wintering, and resident birds, including the critically endangered Bahama Oriole, which appears to depend heavily on this vegetation type during certain life stages.

1 Diverse habitat use during two life stages of the critically Endangered Bahama Oriole (*Icterus*
2 *northropi*): Community structure, foraging, and social interactions

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13 ABSTRACT.--- Our ability to prevent extinction in declining populations often depends
14 on effective management of habitats that are disturbed through wildfire, logging, agriculture, or
15 development. In these disturbed landscapes, the juxtaposition of multiple habitat types can be
16 especially important to fledglings and young birds, which may leave breeding grounds in human-
17 altered habitat for different habitats nearby that provide increased foraging opportunities,
18 reduced competition, and higher protection from predators. In this study, we sought to better
19 understand the importance of habitat diversity to two life stages of the critically endangered
20 Bahama Oriole (*Icterus northropi*), a synanthropic songbird endemic to Andros, The Bahamas.
21 First, we determined the avian species composition and relative abundance of the oriole among
22 three major vegetation types on Andros: Caribbean pine (*Pinus caribaea*) forest, coppice
23 (broadleaf dry forest), and anthropogenic areas, dominated by nonnative vegetation (farmland
24 and developed land). We then compared the foraging strategies and social interactions of two age
25 classes of adult orioles in relation to differential habitat use. Bird surveys late in the oriole's
26 breeding season indicated avian species richness and oriole density were highest in coppice.
27 Some bird species occurring in the coppice and pine forest were never observed in agricultural or
28 residential areas, and may be at risk if human disturbance of pine forest and coppice increases, as
29 is occurring at a rapid pace on Andros. During the breeding season, second-year (SY) adult
30 orioles foraged in all vegetation types, whereas after-second-year (ASY) adults were observed
31 foraging only in anthropogenic areas, where the species nested largely in introduced coconut
32 palms (*Cocos nucifera*). Additionally, SY adults foraging in anthropogenic areas were often
33 observed with an ASY adult, suggesting divergent habitat use for younger, unpaired birds. Other
34 aspects of foraging (vegetation features, food-gleaning behavior, and food items) were similar
35 for the two age classes. Older orioles exhibited relatively higher rates of social interactions

36 (intraspecific and interspecific pooled) in anthropogenic areas, and won more interaction
37 outcomes compared to younger adults. Our findings concur with those of other studies indicating
38 dry broadleaf forest is vitally important to migrating, wintering, and resident birds, including the
39 critically endangered Bahama Oriole, which appears to depend heavily on this vegetation type
40 during certain life stages.

41 *Key words.*---Caribbean, dry tropical forest, synanthropic species, anthropogenic habitat, pine
42 forest

44 Conservation of endangered species often depends on effective management within
45 human-modified landscapes (Gardner et al. 2009). Resource subsidies in anthropogenic areas,
46 such as cultivated plants or discarded food items, influence avian distribution, abundance, and
47 productivity (Faeth et al. 2005). Synanthropic species, which affiliate with humans, often
48 increase in disturbed areas (Kamp et al. 2009, Coulombe et al. 2011), whereas other species,
49 including many Neotropical migrants, may avoid such areas or decline following disturbance
50 (Miller et al. 2007), particularly where much of the canopy is removed (Norris et al. 2009).

51 Some species may be negatively affected by expanding agriculture and development if
52 multiple habitat types are required to sustain viable populations (Cohen and Lindell 2005). The
53 juxtaposition of multiple habitat types can be especially important to fledglings and young birds,
54 which may leave breeding grounds in human-altered habitat for different habitats nearby that
55 provide increased foraging opportunities and higher protection from predators (Cohen and
56 Lindell 2004, Ausprey and Rodewald 2011, Price et al. 2011). Juveniles are often less efficient
57 foragers than adult birds (Heise and Moore 2003; Gall et al. 2013), and may seek habitats with
58 reduced competition from conspecifics. To effectively target conservation efforts, we must
59 therefore understand the relative contribution of each habitat type to each life stage, and by
60 extension, population stability (Dent and Wright 2009).

61 The Bahama Oriole (*Icterus northropi*), a critically endangered island endemic extirpated
62 from Abaco Island in the late 20th century and remaining today only on Andros Island, has
63 contended with profound habitat changes since the arrival of humankind (Steadman et al. 2015,
64 Steadman and Franklin 2015). While logging and human development removed native breeding
65 and foraging habitats (Currie et al. 2005), impacting species sensitive to roads and clearings
66 (Laurance et al. 2009), humans provided novel opportunities for feeding and nesting in the form

67 of introduced plant species (Nickrent et al. 2008). Coconut palms (*Cocos nucifera*), for example,
68 were imported to the region by humans about 500 years ago (Child 1974, Baudouin and Lebrun
69 2009), and have become the oriole's favored nesting habitat (Allen 1890, Baltz 1996, 1997),
70 most likely due to a preference for the tallest trees available within a nest-site (Price et al. 2011).

71 Although largely a synanthropic species associated with human-altered landscapes during
72 the breeding season (Price et al. 2011), the oriole, like other species (Vega Rivera et al. 1998,
73 Graham 2001), may still depend on other vegetation types to sustain various activities throughout
74 its life cycle, and may benefit from foraging in multiple vegetation types (Cohen and Lindell
75 2005), including dry tropical forest (coppice), pine forest, and human-altered (anthropogenic)
76 areas. Dry tropical forest comprises one of the most endangered tropical ecosystems globally due
77 to anthropogenic disturbance (Janzen 1988; Gillespie et al. 2012; Banda et al. 2016). In the
78 Bahamas, dry tropical broadleaf forest (coppice) has decreased due to the effects of forest fires
79 on ecological succession, and forest clearing in the mid-1900's, but has largely recovered since
80 then. However, much of what remains lacks protection and the secondary forest lacks
81 heterogeneity (Myers et al. 2004; Currie et al. 2005), but may still be an important contributor to
82 avian species diversity (Dent and Wright 2009). Recently, coppice loss has accelerated due to
83 development, increased frequency of human-caused fires, and invasion by non-native vegetation
84 during succession (Smith and Vankat 1992; Myers et al. 2004, Koptur et al. 2010, Thurston
85 2010, Carey et al. 2014; see also Larkin et al. 2012).

86 In this study, we sought to better understand the importance of three habitat types to two
87 life stages of the Bahama Oriole. Because interspecific and intraspecific interactions can be
88 influenced by habitat distribution and foraging strategies (Mac Nally and Timewell 2005,
89 Shochat et al. 2010), we needed a better understanding of the avian community structure in

90 habitats used by the oriole. Thus, we began by determining the avian species composition and
91 relative abundance of the oriole among three major vegetation types on Andros: Caribbean pine
92 forest, coppice, and anthropogenic areas. We then compared the foraging strategies and social
93 interactions (both intraspecific and interspecific) of two age classes of adult orioles in relation to
94 differential habitat use.

95

96 METHODS

97 Study Area

98 Andros Island, The Bahamas, comprises a collection of small islands and cays riddled
99 with waterways and bights up to 5 km wide. Andros is dominated on the eastern portion by
100 extensive Caribbean pine forest, with coppice at higher elevations and in patches interspersed
101 within the pine forest. Mangrove, associated with vast tidal wetlands and accessible only by boat,
102 dominates the western half. The pine forest was heavily logged in the mid-1900's (Myers et al.
103 2004), and old logging roads provide the only ground access to the interior. Pine trees in the
104 secondary forest are slender and closely spaced, with an understory of poisonwood (*Metopium*
105 *toxiferum*) and palmetto (*Sabal palmetto*), fern, or shrub (Currie et al. 2005). Townships and
106 agricultural developments are spread along the eastern portion.

107

108 Population Surveys and Observational Effort

109 Other studies have assessed bird composition on Andros during the winter (Currie et al.
110 2005) and early breeding seasons (Lloyd et al. 2010; Price et al. 2011). To evaluate population
111 density and species composition late in the oriole's breeding season, we conducted line transects
112 between 5–18 July 2005 in coppice, pine forest, and anthropogenic areas on North Andros, using

113 methods similar to Emlen (1971, 1977) and Hayes et al. (2004). During this time period we
114 expected some oriole nests would have fledged, while others were initiating second broods. We
115 walked individually or with an assistant at approximately 1 km/hr, surveying 33 transects
116 totaling 19.5 km, with 9.8 km in coppice, 2.4 km in pine forest, and 7.3 km in anthropogenic
117 areas. We recorded all birds identified by sight or vocalization to compare relative and habitat-
118 specific abundance of orioles with other species. Research was approved by the Loma Linda
119 University Institutional Animal Care and Use Committee (Protocol 8120010), and conducted
120 under a Bahamas Ministry of the Environment Research Permit.

121

122 Foraging Behavior

123 We obtained foraging and social interaction data during 17 June–13 July 2007 and 29
124 March–30 May 2009. Total time in direct observation of orioles was approximately 122 hr. To
125 quantify foraging behaviors, we conducted continuous focal observations of individuals for up to
126 2 hr or until the bird flew out of sight. Independence of data was improved by recording the first
127 behavior observed after 10-min intervals, or the first behavior after a location change >10 m,
128 whichever came first. Because foraging birds were often only within eyesight for brief periods of
129 time, resulting in single foraging data points for many birds, we included only the first foraging
130 behavior per bird per day in calculations for statistical analyses. We noted age of the bird as
131 second-year (SY) or after-second-year (ASY) and recorded foraging variables per Remsen and
132 Robinson (1990), including habitat foraged in, location of the bird, substrate fed upon, and food
133 identity. We also noted foliage species in which foraging occurred, and location of the bird in the
134 vegetation, both horizontally (by dividing the tree into visual thirds of inner, middle, outer) and
135 vertically (using a clinometer). Substrates used during foraged were recorded as air, flowers,

136 berries, leaves, twigs, ground, or bark. Foraging tactics were identified as perch gleaning
137 (picking food from a nearby substrate while perched), hang gleaning (picking food from a
138 substrate while hanging upside down), or air-gleaning (plucking insects from the air). We
139 recorded the type of food eaten if it could be identified.

140

141 Social Interactions

142 During the aforementioned focal observations, all intraspecific and interspecific
143 interactions were also noted, per Bowman et al. (1999), as an aerial chase, tree chase, lunge, or
144 usurp. The species and sex (if they could be determined) of the birds were noted, as well as
145 outcome of the interaction, such whether each bird flew away or remained.

146

147 Statistical Analyses

148 We used both parametric and non-parametric tests (Zar 1996), depending on nature of the
149 dependent measure and whether or not assumptions were met. We compared the distribution of
150 individual bird species among the three habitats using Kruskal-Wallis ANOVAs. We compared
151 foraging variables and social interactions between SY and ASY adult orioles using chi-square
152 tests for categorical data and independent-samples *t*-tests for continuous data, with habitat
153 categories collapsed to “anthropogenic habitat” and “not anthropogenic habitat” and data from
154 2007 and 2009 combined due to statistical similarity.

155 We also computed effect sizes, which are largely independent of sample size (in contrast
156 to statistical significance) and more readily compared among different data sets and different
157 studies (Nakagawa and Cuthill, 2007). For Kruskal-Wallis ANOVAs, we calculated eta-squared
158 (η^2) as $\chi^2 / N-1$ (Green and Salkind, 2005), with values of ~ 0.01 , ~ 0.06 , and ≥ 0.14 loosely

159 considered small, medium, and large, respectively (Cohen, 1988). For pairwise comparisons (t -
160 tests), we relied on Cohen's d using Hedges's pooled standard deviation (Nakagawa and Cuthill,
161 2007), with ~ 0.1 , ~ 0.5 , and ≥ 0.8 deemed small, moderate, and large, respectively (Cohen 1988).
162 For tests of proportions (χ^2), we computed Phi (ϕ) for 2×2 and Cramer's V for larger contingency
163 tables, with ~ 0.1 , ~ 0.3 , and ≥ 0.5 considered small, moderate, and large (Cohen 1988). Following
164 Nakagawa (2004), we chose not to adjust alpha for multiple tests. Although some chi-square
165 tests did not meet assumptions of minimal expected frequencies, the effect sizes corresponded
166 well with and supported the interpretations of significance. All analyses were performed using
167 SPSS 17.0 (2008), with alpha of 0.05. Values are presented as mean \pm 1 SE.

168

169

RESULTS

170 Population Densities

171 Avian species richness late in the reproductive season was roughly equivalent in pine
172 forest (24 species) and anthropogenic habitat (26 species), but higher in coppice (35 species,
173 Table 1). Some species clearly associated with one or two habitats, whereas others were
174 generalists; however, transects with zero counts limited statistical power and our ability to
175 identify possible habitat preferences for a number of species, including the oriole ($P = 0.18$, $\eta^2 =$
176 0.11 ; note moderately large effect size). Adult and fledged Bahama Orioles were most numerous
177 in coppice (5.6/km), followed by anthropogenic habitat (1.2/km). Although orioles were not
178 detected in pine forest during these surveys, they were occasionally observed in this habitat
179 during subsequent work (Price et al. 2011).

180 The density of the Bahama Oriole can be compared to that of other species in Table 1,
181 where some structuring of bird communities is evident. Thick-Billed Vireo (*Vireo crassirostris*)

182 was significantly associated with coppice. Black-Faced Grassquit (*Tiaris bicolor*), Blue-Gray
183 Gnatcatcher (*Poliophtila caerulea*), Greater Antillean Bullfinch (*Loxigilla violacea*), Pine Warbler
184 (*Dendroica pinus*), and Western Spindalis (*Spindalis zena*) were significantly associated with
185 pine forest. Cuban Emerald (*Chlorostilbon ricordii*), Eurasian Collared Dove (*Streptopelia*
186 *decaocto*), Gray Kingbird (*Tyrannus dominensis*), Laughing Gull (*Leucophaeus atricilla*),
187 Northern Mockingbird (*Mimus polyglottos*), Smooth-Billed Ani (*Crotophaga ani*), and Turkey
188 Vulture (*Cathartes aura*) were significantly more likely to be found in anthropogenic habitat.
189 Bananaquit (*Coereba flaveola*) was significantly more likely to be found in pine forest and
190 anthropogenic habitat.

191

192 Foraging

193 Of the foraging variables listed in Table 2, only habitat in which individuals foraged
194 differed significantly between SY and ASY adults ($P = 0.003$, $\Phi = 0.58$). Whereas SY adults (N
195 $=15$) foraged in coppice, pine forest, and anthropogenic habitat, ASY adults ($N =12$) were
196 observed foraging only in anthropogenic habitat. Those SY adults foraging in anthropogenic
197 habitat were often paired with an ASY adult (six of seven individuals). Two additional variables
198 showed moderately large effect sizes (Table 2), suggesting that ASY adults are more general in
199 foraging location and in substrate use, whereas SY birds are more likely to forage near the
200 middle of vegetation ($P = 0.13$, $V = 0.40$) from leaves, twigs, or bark ($P = 0.14$, $V = 0.45$). Both
201 age groups foraged in multiple plant species, with no clear preference (data not shown). Most
202 food was obtained through perch-gleaning (93% of 27 observations), on leaves and twigs (60%
203 of 27 observations) in the middle of a branch (46% of 27 observations). Both SY and ASY adults
204 were observed air-gleaning and hang-gleaning, although not all of these observations were

205 included in statistical analysis due to non-independence of data points. Birds were observed
206 eating insects (89% of 27 observations) and berries (11%). Other food items included a
207 Caribbean hermit crab (*Coenobita clypeata*), which a SY bird unsuccessfully attempted to ingest,
208 and an endemic brown anole (*Norops sagrei*), which was fed to hatchlings (Price et al. 2011).
209 Although orioles foraged among flowers and may have ingested nectar, we could not ascertain
210 whether their target was the nectar or insects among the flowers.

211

212 Social Interactions

213 Intraspecific and interspecific interactions were rare, with only 15 social interactions
214 witnessed (0.12/hr of direct oriole observation; Table 3), limiting statistical power. While no
215 comparisons were statistically significant, the large effect sizes suggested that social interactions
216 were more likely to occur in anthropogenic habitat for ASY birds and in other habitats (pine or
217 coppice) for SY birds ($P = 0.077$, $V = 0.53$; note large effect size). Older (ASY) birds were also
218 more likely to “win” altercations than SY birds ($P = 0.077$, $V = 0.53$). The avian species that
219 orioles interacted with (intraspecific vs. interspecific; $P = 0.74$, $V = 0.08$) and the approximate
220 height above ground of the interaction ($P = 0.67$, $d = 0.11$) were similar for SY and ASY birds,
221 with small effect sizes.

222 Intraspecific competitive interactions between orioles were especially scarce (26.7% of
223 15 total interactions, and only 0.03/hr of direct oriole observation). In 2009, at the Atlantic
224 Undersea Test and Evaluation Center (AUTECE) where the highest density of orioles on North
225 Andros was observed, two pairs of orioles with hatched chicks nested within 200 m of one
226 another. One oriole from each pair engaged in an aerial chase at the presumed territory boundary.
227 No physical contact was made, although the orioles sang from their respective territories for

228 approximately 30 min following the encounter. On two other occasions, near the beginning of
229 the nesting season, ASY adult oriole pairs were observed chasing SY adults, sometimes tussling
230 with them to the ground.

231 Several interspecific interactions were observed. Orioles engaged a LaSagra's Flycatcher
232 (*Myiarchus sagrae*), a Smooth-Billed Ani, a Red-Legged Thrush (*Turdus plumbeus*), and a
233 House Sparrow (*Passer domesticus*) pair when these birds independently flew into an oriole nest
234 tree. All were chased away except for the House Sparrow pair, which shared a nest tree with an
235 oriole pair. Orioles chased a Shiny Cowbird (*Molothrus bonariensis*) away from their nest area.
236 When foraging on one occasion, orioles did not interact with nearby cowbirds. Northern
237 Mockingbirds with a nest nearby chased away Bahama Orioles that strayed too close.

238 We observed several cooperative efforts to chase away potential predators. On one
239 occasion, an oriole and three unidentified passerines chased a Red-tailed Hawk (*Buteo*
240 *jamaicensis*) from its perch in a Caribbean pine tree. On another occasion, one ASY and two SY
241 orioles lunged repeatedly at a Yellow-crowned Night Heron (*Nyctanassa violacea*), which only
242 rarely raids nests (Watts 2011), for over an hour without displacing it. On two occasions, Gray
243 Kingbirds whose territories overlapped with oriole territories chased away Turkey Vultures.

244

245 DISCUSSION

246 Population Densities and Estimates

247 Coppice, pine forest, and anthropogenic habitats contained both habitat-specialists and
248 habitat-generalists. As our surveys were conducted during the breeding season for many of the
249 species surveyed, the habitat distributions may not represent a complete picture of the habitats
250 important to long-term survival of both juveniles and adults of the resident species. The Bahama

251 Oriole appears to be somewhat of a habitat-generalist, but this becomes apparent only when
252 considering both breeding and non-breeding periods. The oriole strongly associates with
253 anthropogenic habitats during the breeding season, as it prefers to nest in the tallest palms
254 available, which are now introduced coconut palms in the vicinity of human residential areas
255 (Baltz 1996, 1997; Price et al. 2011). The oriole likely benefits also from increased foraging
256 opportunities in other cultivated plants and ready access to adjacent coppice and pine forest
257 foraging grounds. Our survey results late in the breeding season, however, suggest that fledglings
258 with their parents move out of anthropogenic habitats and into coppice habitat shortly after
259 departure from nests. We also observed a high number of SY individuals foraging and
260 interacting socially in coppice during the breeding season. Moreover, during winter surveys,
261 Currie et al. (2005) detected the orioles only in coppice and agricultural areas, and did not
262 observe them in pine forest lacking a coppice understory. Thus, these studies illustrate the
263 contrasting needs of these birds for anthropogenic habitat, which is relied on heavily during
264 nesting, and coppice, which appears to be important for fledglings, younger birds, and perhaps
265 birds of all ages outside of the breeding season. Unfortunately, coppice is often cleared by
266 humans for agriculture and residential development (Smith and Vankat 1992), and is currently
267 undergoing rapid decimation on South Andros (Lloyd and Slater 2010, Thurston 2010). This
268 could decrease foraging opportunities for fledging chicks.

269 A handful of species were significantly more likely to be found in human-disturbed
270 anthropogenic habitat. These included the Cuban Emerald, Eurasian Collared Dove, Gray
271 Kingbird, Laughing Gull, Northern Mockingbird, Smooth-Billed Ani, and Turkey Vulture.
272 Turkey Vultures, which frequent locations of trash disposal, clearly benefit from human-
273 provided food resources. Other forms of resource subsidies include cultivated fields, imported

274 plants, and fresh water (Faeth et al. 2005). Birds associating with human-disturbed habitats may
275 also be attracted to the open spaces or edges created as land is cleared for development (Hawrot
276 and Nieme1996). The frequent occurrence of Laughing Gulls in anthropogenic habitat may be in
277 large part because of the proximity of anthropogenic areas to coastal areas. Several of these
278 birds, including Laughing Gulls and Turkey Vultures, may opportunistically act as predators on
279 newly-fledged oriole chicks. Others, such as the Northern Mockingbird, may provide
280 competition for food items.

281 Some species, including several endemic species, were never observed in agricultural or
282 residential areas, and may be at risk if human disturbance of coppice and pine forest increases.

283 Among the resident species, the Bahama Mockingbird (*Mimus gundlachi*), Bahama
284 Yellowthroat (*Geothlypis rostrata*), Greater Antillean Pewee (*Contopus caribaeus*), Greater
285 Antillean Bullfinch (*Loxigilla violacea*), Key West Quail Dove (*Geotrygon chrysie*), La Sagra's
286 Flycatcher, Mangrove Cuckoo (*Coccyzus minor*), and Pine Warbler (*Dendroica pinus*) were
287 never observed in anthropogenic habitat during this study, or during subsequent observations.

288

289 Foraging

290 Food availability and diet composition of the Bahama Oriole may change throughout the
291 year. One study found protein-rich invertebrates to be the most common food delivered to
292 hatchlings of the closely related Cuban Oriole (*I. melanopsis*), Hispaniolan Oriole (*I.*
293 *dominicensis*), and Puerto Rican Oriole (*I. portoricensis*), whereas orioles outside of the breeding
294 season more often fed on carbohydrate-rich fruit, flowers, and nectar (Garrido et al. 2005).
295 Insects generally have higher densities in pine forest and coppice habitats, whereas fruit and
296 nectar are more abundant in recently disturbed areas (Currie et al. 2005). Thus, we expected

297 breeding orioles to forage preferentially in pine forest and coppice, and non-breeding orioles to
298 forage more often in anthropogenic habitat. Our breeding season observations of the oriole's diet
299 composition corresponded with previous studies of related orioles in general composition, as it
300 included fruit, nectar, arthropods, and occasional small vertebrates (Garrido et al. 2005).
301 Foraging method was also consistent with expectations, as most food was obtained through
302 perch-gleaning (93% of 27 observations), a simple and relatively inexpensive method in terms of
303 energy (Vanderwerf 1993). Contrary to expectations, however, we found that lone SY orioles
304 foraged only in coppice and pine forest, whereas ASY adults were observed foraging only in
305 anthropogenic habitat. The oriole's proclivity for nesting in coconut palms (Price et al. 2011),
306 planted primarily in association with human development, may influence the foraging habits of
307 ASY adults, and sufficient protein-rich sources may be present. Interestingly, SY orioles paired
308 with an ASY adult almost always foraged in anthropogenic habitat (six of seven observations).
309 Lone SY adults may be forced out of the most desirable habitat due to despotism (Railsback et
310 al. 2003), whereas those paired with older birds, either for breeding or through delayed dispersal,
311 potentially benefit from association with an established territory. Thus, the difference in foraging
312 habitats between SY and ASY adult orioles may have reflected social structure more so than
313 differential food availability among habitats.

314

315 Social Interactions

316 Older (ASY) orioles interacted more often with other birds in anthropogenic habitat and
317 "won" altercations more often than younger (SY) orioles. The ASY birds in anthropogenic
318 habitat were often nesting or feeding young, and may have had more motivation to defend
319 territories or offspring than SY individuals without a territory to defend. Young adults may also

320 lack the experience to outcompete other birds who challenge them, making it more likely for
321 them to leave an area to avoid more serious altercations.

322 Intraspecific competitive interactions between orioles were rare, probably due to the low
323 density of the Bahama Oriole population. Competitive interactions between ASY adults were
324 only observed in areas of better palm health and correspondingly higher oriole density (c.f., Price
325 et al. 2011). Aggressive interactions between ASY and SY adults may have involved parents
326 chasing away offspring from a previous brood prior to beginning a new breeding season, or the
327 SY adults may have been young males encroaching on the territories of ASY adults. Long-term
328 studies of individuals marked during their hatch year are needed to elucidate interactions within
329 family groups and during recruitment of juveniles.

330

331 Conservation Implications

332 *Dry tropical forest.* Our findings concur with other studies that indicate coppice is vitally
333 important to resident, migrating, and wintering birds in the Bahamas, including the critically
334 endangered Bahama Oriole (Raffaele et al. 2003, Lloyd and Slater 2010). Our surveys found the
335 highest number of avian species during the breeding season in coppice (35 versus 24 in pine
336 forest and 26 in anthropogenic habitat). Winter survey results on Andros by Currie et al. (2005)
337 similarly detected the highest total number of species in coppice and shrubby field habitats (26–
338 27 versus 19–22 species in pine-dominated habitats; anthropogenic habitats were not included in
339 their study). Young orioles often foraged in coppice, and fledglings leaving nests in
340 anthropogenic habitat fledged to coppice (Price et al. 2011). As all species interact with one or
341 more other species in food webs via competition, predation, parasitism, or mutualism, future
342 studies should elucidate interactions within these habitats, as conservation efforts more likely to

343 succeed when these complex food web interactions and the ways human activities alter them are
344 understood (Faeth et al. 2005).

345 *Caribbean pine forest.* Caribbean pine forests on Andros, logged heavily throughout the
346 last century, have returned as homogenous even-aged stands with closely-spaced, slender trees
347 (Currie et al. 2005). This has likely decreased avian diversity compared with old-stand forests, as
348 snags, cavity trees, hardwoods, and large downed woody material are largely absent within
349 secondary-growth pine forests (Thill and Koerth 2005). Hardwood forests purposefully managed
350 to retain or increase large live trees, snags, and coarse woody debris have increased densities of
351 many birds of conservation concern (Twedt and Somershoe 2009). Young Bahama Orioles often
352 feed in the pine forest (this study), and adults likely nest at low density in areas where a palm
353 understory exists (Price et al. 2011). Given the importance of the wide swaths of Caribbean pine
354 forest to migratory, wintering, and permanent resident species, conservation plans should
355 consider management of pine forests to increase heterogeneity.

356 *Anthropogenic areas.* Not all avian species will decline with human disturbance, and
357 some may even benefit from resource subsidies and increases in open and edge habitats,
358 including those within anthropogenic areas (Werner et al. 2007, Kamp et al. 2009, Coulombe et
359 al. 2011). The Bahama Oriole uses anthropogenic habitat during the breeding season, where it
360 selects nest sites in the tallest available palm trees (Price et al. 2011). Breeding in anthropogenic
361 areas may result in higher levels of nest parasitism from Shiny Cowbirds (Baltz 1996, 1997,
362 Price et al. 2011), but the benefits of greater nest height for predator avoidance might offset any
363 such disadvantage (c.f. Burhans and Thomson 2006). Adult orioles in particular appear to benefit
364 from foraging in this habitat during the breeding season (this study).

365 We believe the Bahama Oriole requires multiple vegetation types throughout its life
366 history and will benefit from careful management of both coppice, which is currently at high risk
367 of rapid loss due to increasing development on Andros (Lloyd and Slater 2010; Thurston 2010),
368 and pine forest, which has become more homogenous following deforestation and frequent
369 human-caused forest fires (Currie et al. 2005). Planning for future development on Andros
370 (Inter-American Development Bank 2014) should make a concerted effort to minimize
371 disturbance of these critical habitats.

372

373

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375

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378

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519 Table 1. Relative density by habitat (individuals/km) of birds on North Andros, The Bahamas,
 520 from 33 line transects during June and July of 2005, with Kruskal-Wallis ANOVA results (Chi-
 521 square and *P* values) and eta-squared (η^2) effect sizes.

522

Species	Pine	Coppice	Anthropogenic	χ^2_2	<i>P</i>	η^2
	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$			
American Kestrel (<i>Falco sparverius</i>)	0.0	0.0	0.9 ± 0.8	3.94	0.14	0.12
Bahama Mockingbird (<i>Mimus gundlachii</i>)	1.4 ± 0.8	4.4 ± 2.3	0.0	6.89	0.032	0.22
Bahama Oriole (<i>Icterus northropi</i>)	0.0	5.6 ± 4.4	1.2 ± 0.6	3.44	0.18	0.11
Critically Endangered						
Bahama Swallow (<i>Tachycineta cyaneoviridis</i>)	0.5 ± 0.4	2.0 ± 1.2	1.5 ± 1.1	0.92	0.63	0.03
Endangered						
Bahama Woodstar (<i>Calliphlox evelynae</i>)	0.0	0.2 ± 0.2	0.1 ± 0.1	1.74	0.42	0.05
Bahama Yellowthroat (<i>Geothlypis rostrata</i>)	0.2 ± 0.2	1.2 ± 0.6	0.0	6.83	0.033	0.21
Bananaquit (<i>Coereba flaveola</i>)	2.4 ± 0.8	1.1 ± 0.8	2.9 ± 0.9	4.24	0.12	0.13
Black-and-white Warbler ^a (<i>Mniotilta varia</i>)	0.0	0.2 ± 0.2	0.0	1.67	0.44	0.05
Black-faced Grassquit (<i>Tiaris bicolor</i>)	15.4 ± 4.6	5.5 ± 2.3	0.3 ± 0.2	13.05	0.001	0.41
Blue-gray Gnatcatcher (<i>Poliioptila caerulea</i>)	10.2 ± 2.5	4.6 ± 2.4	1.1 ± 0.9	10.56	0.005	0.33

Black-whiskered Vireo (<i>Vireo altiloquus</i>)	8.3 ± 2.6	12.5 ± 4.2	2.5 ± 1.0	3.81	0.15	0.12
Common Ground Dove (<i>Columbina passerine</i>)	2.1 ± 1.1	2.2 ± 1.0	5.4 ± 2.2	2.93	0.23	0.09
Greater Antillean Pewee (<i>Contopus caribaeus</i>)	0.6 ± 0.6	0.2 ± 0.1	0.0	2.97	0.23	0.09
Cuban Emerald (<i>Chlorostilbon ricordii</i>)	1.3 ± 1.1	5.3 ± 2.6	5.1 ± 1.4	6.48	0.039	0.20
Eurasian Collared Dove ^b (<i>Streptopelia decaocto</i>)	0.8 ± 0.6	1.5 ± 0.9	7.2 ± 3.7	5.59	0.06	0.17
Gray Kingbird (<i>Tyrannus dominensis</i>)	2.4 ± 1.7	5.5 ± 4.5	5.0 ± 1.7	6.00	0.050	0.19
Great Lizard Cuckoo (<i>Saurothera merlini</i>)	0.0	0.2 ± 0.1	0.3 ± 0.3	1.53	0.47	0.05
Greater Antillean Bullfinch (<i>Loxigilla violacea</i>)	6.0 ± 3.0	0.4 ± 0.4	0.0	8.20	0.017	0.26
Hairy Woodpecker (<i>Picoides villosus</i>)	4.2 ± 2.0	3.2 ± 1.6	0.1 ± 0.1	5.74	0.06	0.18
House Sparrow ^b (<i>Passer domesticus</i>)	0.0	1.7 ± 1.7	0.5 ± 0.5	0.81	0.67	0.03
Key West Quail Dove (<i>Geotrygon chrysie</i>)	0.0	0.8 ± 0.8	0.0	3.44	0.18	0.11
Killdeer (<i>Charadrius vociferous</i>)	0.0	0.0	1.1 ± 0.9	3.94	0.14	0.12
La Sagra's Flycatcher (<i>Myiarchus sagrae</i>)	0.8 ± 0.7	1.4 ± 0.7	0.0	4.09	0.13	0.13
Laughing Gull (<i>Leucophaeus atricilla</i>)	0.0	1.3 ± 1.1	3.0 ± 1.0	10.17	0.006	0.32

Loggerhead Kingbird						
<i>(Tyrannus caudifasciatus)</i>	0.0	0.0	0.0	0.00	1.00	0.00
Mangrove Cuckoo						
<i>(Coccyzus minor)</i>	0.0	1.1 ± 1.1	0.0	1.67	0.44	0.05
Northern Bobwhite ^b						
<i>(Colinus virginianus)</i>	2.3 ± 1.3	0.4 ± 0.3	0.0	4.35	0.11	0.14
Near Threatened						
Northern Mockingbird						
<i>(Mimus polyglottos)</i>	0.9 ± 0.7	2.2 ± 2.2	7.3 ± 1.8	15.34	0.001	0.48
Pine Warbler						
<i>(Dendroica pinus)</i>	2.6 ± 1.1	0.5 ± 0.4	0.0	6.88	0.032	0.22
Red-legged Thrush						
<i>(Turdus plumbeus)</i>	1.2 ± 0.6	1.9 ± 0.8	0.0	5.76	0.06	0.18
Red-winged Blackbird						
<i>(Agelaius phoeniceus)</i>	0.0	1.7 ± 1.7	0.1 ± 0.1	0.81	0.67	0.03
Rock Dove ^b						
<i>(Columba livia)</i>	0.2 ± 0.2	0.3 ± 0.3	2.2 ± 2.1	0.50	0.78	0.02
Shiny Cowbird						
<i>(Molothrus bonariensis)</i>	0.2 ± 0.2	0.0	0.3 ± 0.2	3.69	0.16	0.12
Smooth-billed Ani						
<i>(Crotophaga ani)</i>	0.0	0.7 ± 0.5	8.0 ± 6.3	8.08	0.018	0.25
Thick-billed Vireo						
<i>(Vireo crassirostris)</i>	0.3 ± 0.3	6.4 ± 1.7	2.5 ± 0.8	11.68	0.003	0.37
Turkey Vulture						
<i>(Cathartes aura)</i>	0.0	3.4 ± 2.4	5.4 ± 1.5	10.20	0.006	0.32
Western Spindalis						
<i>(Spindalis zena)</i>	7.0 ± 1.7	3.3 ± 1.3	0.3 ± 0.3	11.22	0.004	0.35
White-crowned Pigeon						
	5.0 ± 2.5	5.5 ± 4.4	0.3 ± 0.2	4.46	0.11	0.14

(Patagioenas leucocephala)

Zenaida Dove

(Zenaida aurita)

0.0 1.1 ± 1.1 0.0 1.67 0.44 0.05

523

524 ^a Non-resident migratory species

525 ^b Introduced species

526

528 Table 2. Comparisons of foraging variables between second-year (SY) and after-second-year
 529 (ASY) Bahama Oriole (*Icterus northropi*) adults, with chi-square and *t*-test results.

530

Foraging Variable	SY	ASY	Test statistic (df)	<i>P</i>	Effect size ^a
Habitat					
Anthropogenic	<i>N</i> = 7	<i>N</i> = 12	$\chi^2_1 = 9.10$	0.003	$\Phi = 0.58$
Not anthropogenic	<i>N</i> = 8	<i>N</i> = 0			
Height ($\bar{x} \pm SE$)	5.2 \pm 0.4	4.9 \pm 0.9	$t_{25} = 0.32$	0.75	<i>d</i> = 0.19
Horizontal location					
Inner	<i>N</i> = 3	<i>N</i> = 5	$\chi^2_2 = 4.04$	0.13	<i>V</i> = 0.40
Middle	<i>N</i> = 9	<i>N</i> = 3			
Outer	<i>N</i> = 2	<i>N</i> = 4			
Substrate					
Air	<i>N</i> = 1	<i>N</i> = 0	$\chi^2_3 = 5.48$	0.14	<i>V</i> = 0.45
Berries	<i>N</i> = 0	<i>N</i> = 2			
Flowers	<i>N</i> = 3	<i>N</i> = 5			
Leaves, twigs or bark	<i>N</i> = 11	<i>N</i> = 5			
Behavior					
Air-gleaning	<i>N</i> = 1	<i>N</i> = 0	$\chi^2_2 = 1.73$	0.42	<i>V</i> = 0.25
Hang-gleaning	<i>N</i> = 1	<i>N</i> = 0			
Perch-gleaning	<i>N</i> = 13	<i>N</i> = 12			
Food item					
Berries	<i>N</i> = 1	<i>N</i> = 2	$\chi^2_1 = 0.68$	0.41	$\Phi = 0.16$

Insects	$N = 14$	$N = 10$
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531

532 ^a Effect sizes: Phi (Φ), Cohen's d , and Cramer's V ; see Methods.

533 Table 3. Comparisons of social interactions and their outcomes between second-year (SY) and
 534 after-second-year (ASY) Bahama Oriole (*Icterus northropi*) adults, with Chi-square and *t*-test
 535 results.

536

Variable	SY	ASY	Test statistic (df)	<i>P</i>	Effect size ^a
Habitat ^{b,c}					
Anthropogenic	<i>N</i> = 1	<i>N</i> = 9			
Coppice	<i>N</i> = 2	<i>N</i> = 1	$\chi^2_1 = 4.26$	0.077	<i>V</i> = 0.53
Pine Forest	<i>N</i> = 1	<i>N</i> = 1			
Outcome ^b					
Oriole won	<i>N</i> = 0	<i>N</i> = 7			
Oriole lost	<i>N</i> = 4	<i>N</i> = 4	$\chi^2_1 = 4.77$	0.077	$\Phi = 0.56$
Species ^d					
Bahama Oriole	<i>N</i> = 1	<i>N</i> = 2			
Northern Mockingbird	<i>N</i> = 1	<i>N</i> = 3			
La Sagra's Flycatcher	<i>N</i> = 0	<i>N</i> = 1			
Red-Legged Thrush	<i>N</i> = 1	<i>N</i> = 0			
Red-Tailed Hawk	<i>N</i> = 0	<i>N</i> = 1			
Shiny Cowbird	<i>N</i> = 0	<i>N</i> = 1	$\chi^2_1 = 0.09$	0.74	<i>V</i> = 0.08
House Sparrow	<i>N</i> = 0	<i>N</i> = 1			
Smooth-Billed Ani	<i>N</i> = 0	<i>N</i> = 1			
Yellow-Crowned	<i>N</i> = 1	<i>N</i> = 1			
Night-Heron					

Height above ground	9.2 ± 2.3	8.8 ± 0.9	$t_{13} = 0.17$	0.67	$d = 0.11$
$(\bar{x} \pm SE)$					

537

538 ^a Effect sizes: Phi (Φ), Cohen's d , and Cramer's V ; see Methods.539 ^b Intraspecific and interspecific interactions were pooled for analyses.540 ^c Habitat type was collapsed to "anthropogenic" and "not anthropogenic" for analysis.541 ^d Species was collapsed to "intraspecific" (oriole) and "interspecific" (non-oriole) for analysis.

542