

City University of New York (CUNY)

CUNY Academic Works

Publications and Research

Hunter College

2015

A Generalist Brood Parasite Modifies Use of a Host in Response to Reproductive Success

Matthew I M Louder
East Carolina University

Wendy M. Schelsky
University of Illinois at Urbana-Champaign

Amber N. Albores
University of Illinois at Urbana-Champaign

Jeffrey P. Hoover
University of Illinois at Urbana-Champaign

[How does access to this work benefit you? Let us know!](#)

More information about this work at: https://academicworks.cuny.edu/hc_pubs/45

Discover additional works at: <https://academicworks.cuny.edu>

This work is made publicly available by the City University of New York (CUNY).
Contact: AcademicWorks@cuny.edu

A generalist brood parasite modifies use of a host in response to reproductive success

Matthew I. M. Louder^{1,2*}, Wendy M. Schelsky², Amber N. Albores^{1,2}, Jeffrey P. Hoover²

¹Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL, USA

²Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, IL, USA

*Correspondence: Matthew I. M. Louder

mckimlouder@gmail.com

Current address: Department of Biology, East Carolina University, Greenville, NC, USA

Department of Psychology, Hunter College, CUNY, New York, NY, USA

1 **ABSTRACT**

2 Avian obligate brood parasites, which rely solely on hosts to raise their young, should choose the
3 highest quality hosts to maximize reproductive output. Brown-headed cowbirds (*Molothrus ater*) are
4 extreme host generalists, yet female cowbirds could use information based on past reproductive outcomes
5 to make egg-laying decisions thus minimizing fitness costs associated with parasitizing low quality hosts.
6 We use a long-term (21 years) nest box study of a single host, the prothonotary warbler (*Protonotaria*
7 *citrea*), to show that local cowbird reproductive success, but not host reproductive success, was positively
8 correlated with the probability of parasitism the following year. Experimental manipulations of cowbird
9 success corroborated that female cowbirds make future decisions about which hosts to use based on
10 information pertaining to past cowbird success, both within and between years. The within-year pattern,
11 in particular, points to local cowbird females selecting hosts based on past reproductive outcomes. This,
12 coupled with high site fidelity of female cowbirds between years, points to information use, rather than
13 cowbird natal returns alone, increasing parasitism rates on highly productive sites between years.

14

15 **Keywords:** brood parasitism; cognition and reproduction; cowbird; host selection; reproductive
16 performance information; statistical decision theory

17

18 **INTRODUCTION**

19 Obligate avian brood parasites, species that lay their eggs in the nests of heterospecifics, serve as
20 a valuable resource to investigate host-parasite dynamics and coevolutionary processes [1-3]. Likewise,
21 from parasitic species that specializes on a single host species to extreme host generalists, the degree of
22 host specialization among avian brood parasites has intrigued evolutionary biologists [4]. Parasites are
23 often faced with variation in the fitness potential of hosts, both among host species and within a single
24 host across the landscape [2]. To maximize fitness, brood parasitic females should prefer the host(s) best
25 at raising parasitic offspring [5-8] by factoring in host defences, availability, and compatibility. As host
26 defences evolve, coevolutionary theory predicts that avian brood parasites increase in host specificity [9,

27 10]. The brown-headed cowbird (*Molothrus ater*) (cowbirds hereafter), is an extreme host generalist
28 known to parasitize more than 220 species throughout its range [11, 12]. The degree to which female
29 cowbirds select hosts based on the variation in fitness potential is poorly known [13, 14]. While hosts
30 have been observed to modify their behaviour in response to past interactions with brood parasites [15-
31 18], obligate interspecific parasites modifying their use of hosts in response to previous reproductive
32 success has not been demonstrated.

33 The quality of potential hosts for cowbirds is highly variable, but potentially predictable,
34 depending on the likelihood that a particular host species can recognize and reject parasitic eggs [1] or is
35 in some way incompatible with raising a parasitic egg or chick [19]. For example, of the ~220 parasitized
36 species, approximately 140 have successfully raised cowbird offspring [11]. Interspecific brood parasites
37 could enhance reproductive success by preferring species, locations or individuals that fledged offspring
38 (host or parasitic) in the recent past [e.g. 20, 21]. Similarly, host success could be an indirect cue of host
39 quality in systems where cowbird success is principally dependent on nest predation [22]. When
40 reproductive success is predictable, reproductive performance is among the most reliable sources of
41 biological information, enabling individuals to enhance fitness by minimizing uncertainty associated with
42 breeding in heterogeneous environments [23, 24]. Female brown-headed cowbirds, faced with variation in
43 the fitness potential among reproductive decisions, could draw upon the outcomes of past breeding
44 experiences or observations of conspecifics and heterospecifics to maximize fitness within a given
45 environment (i.e. use personal experience or social information).

46 Despite host generalism observed at the species-level, microsatellite DNA markers revealed
47 evidence of preferences for particular hosts within individual female cowbirds in several populations [25-
48 27]. Egg laying decisions of inexperienced female cowbirds, either young individuals or those recently
49 dispersed to novel habitats, may follow a fairly indiscriminate pattern [28]. If the success of parasitized
50 nests is monitored, however, subsequent decisions to use particular hosts could follow statistical decision
51 theory where prior preferences are refined to match information collected by sampling the environment
52 [29]. Radio telemetry and genetic studies of female cowbirds also indicate high breeding site and home

53 range (primary egg-laying area) fidelity both within and between years [26, 30] which would allow
54 females to gather information and use it in subsequent breeding decisions. Cowbird females are equipped
55 with impressive spatial memories [31, 32] and also monitor host nest contents, both before and after
56 parasitism, to time the laying of eggs and ensure their acceptance by the host [33]. Parasitized nest sites
57 are often parasitized again in subsequent attempts [34, 35], potentially indicating preferences for
58 particular individual hosts. Evidence of preferences for particular hosts, in combination with the
59 monitoring of host nests and site fidelity within cowbird populations, suggests cowbirds could improve
60 future reproductive success by incorporating their own reproductive experience or the reproductive
61 success of conspecifics into parasitism decisions.

62 Variation in anti-parasite strategies, microhabitat nesting structure, timing of breeding and
63 abundance among potential host species contributes to the egg laying decisions of generalist brood
64 parasites [2]. Studying the parasitism frequencies within a single host, therefore, would control for the
65 between-species variation that may obscure any patterns in rates of parasitism associated with parasites
66 using past reproductive performance to make egg laying decisions. Investigations of the parasitism
67 frequencies within a single host have revealed increased parasitism rates for host traits (e.g. nest quality,
68 body condition and social dominance) that may be correlated with the host's ability to successfully raise
69 parasitic offspring [reviewed in 36, 37]. However, it remains unclear whether the past reproductive
70 experiences of individual brood parasites, rather than fixed preferences for the host traits themselves,
71 serve as a cue that influences the use of hosts within interspecific brood parasites.

72 In this study, we used a long-term (21 years) nest box dataset from a highly suitable host of
73 brown-headed cowbirds, the prothonotary warbler (*Protonotaria citrea*; warbler hereafter), to investigate
74 the factors influencing cowbird parasitism. Here, we test if the warblers' ability to successfully produce
75 cowbird and/or warbler offspring influences the probability of cowbird parasitism in subsequent breeding
76 attempts. From a cowbird's perspective, the fledging of cowbirds is likely a better signal of host quality
77 than the fledging of host offspring; therefore, we hypothesized that parasitism frequency would increase
78 in response to cowbird fledging success rather than warbler fledging success. First, we predicted that as

79 the number of cowbirds fledging per warbler nest (i.e. cowbird productivity) on a site increased, the
80 following year's probability of cowbird parasitism for warblers on that site would increase, whereas the
81 number of warblers fledging per nesting attempt on a site would have relatively little influence on the
82 rate of future cowbird parasitism. To determine whether the information that is used has effects on
83 parasitism decisions the following year that extend beyond individual nest boxes parasitized previously,
84 we investigated the influence of cowbird productivity on the parasitism status of individual nest boxes
85 used in consecutive years. If female cowbirds use reproductive performance information for subsequent
86 parasitism decisions, we would predict that study-site-specific cowbird success in one year would be
87 positively correlated with the following year's probability of parasitism both for nest boxes that had and
88 had not been parasitized the previous year. Next, by excluding nest predators and then directly
89 manipulating the reproductive success of cowbirds via experimental egg removal, we accounted for
90 potential confounds that cowbirds may use as predictors of reproductive success, such as warbler quality,
91 predation risk or food abundance. Compared to parasitized nests that successfully fledged cowbird
92 offspring, we predicted that experimentally removing cowbird eggs would decrease the probability of
93 parasitism for the subsequent nesting attempts, both between years and between multiple nesting attempts
94 within the same year.

95 **METHODS**

96 **(a) Study species and field methods**

97 The study was conducted over a 21-year period (1994 to 2014) in the Cache River Watershed in
98 southern Illinois, United States (37°18'N, 88°58'W). Here the prothonotary warbler, a territorial and
99 socially monogamous Neotropical migratory songbird [38] that lacks any known anti-parasite defences
100 [39], uses nest boxes that provide easy access for monitoring parasitized nests. Study sites were located in
101 agriculturally fragmented patches of forested sloughs and floodplains with bald cypress (*Taxodium*
102 *distichum*) and tupelo (*Nyssa aquatica*) swamps, within a 192-km² portion of the watershed. Warbler
103 young are fed an insectivorous diet by both parents that is compatible with the diet required to raise
104 cowbird young [40]. Cowbird young are competitive for provisioned food because they are larger than

105 warbler young throughout the nestling and fledgling stage. Despite a high rate of cowbird parasitism
106 (~60% of nests) and the cowbird's larger size, the warblers are often double-brooded and capable of
107 raising both cowbird and host nestlings in each nesting attempt [41, 42].

108 Each year we set up and monitored approximately 1000 warbler nest boxes across 21 sites
109 (individual patches of suitable breeding habitat for warblers separated by more than 1 km of non-suitable
110 habitat). Nest boxes were made from modified 1.9 L beverage cartons and placed on trees about 1.7 m
111 above the ground in suitable habitat. Nest boxes were spaced an average of 50 m apart, and openings in
112 boxes were made to be the average diameter (44 mm) of warbler nests in natural cavities allowing
113 cowbird access to each nest. Study sites where the opening size of nest boxes was reduced to exclude
114 parasitism by cowbirds were not included in our analyses. We monitored boxes every 3-5 days from late
115 April to early August. The status of each nesting attempt was recorded, including the number of warbler
116 and cowbird eggs, nestlings, and the number of cowbird eggs that were removed. We considered nestlings
117 to have fledged if they reached 10-11 days of age and the nest was empty and intact on the subsequent
118 visit. Additional evidence of fledging included the presence of trampled droppings in the nest, alarm calls
119 from adults, and observations of appropriately-aged fledglings in the territory. Adult warblers were
120 captured and fitted with a unique colour-band combination and a numbered aluminum band. The
121 identities of ca. 90% of the warbler adults from each nesting attempt were recorded by either capturing
122 individuals or visual identification.

123 **(b) Study-site-specific cowbird reproductive success**

124 We first investigated a nest box dataset including study sites/years where cowbird eggs were not
125 removed ($n = 1458$). To test whether the site-specific production of warbler or cowbird offspring in one
126 year (t) best predicted site-specific cowbird parasitism in the following year ($t+1$), we included site-
127 specific warbler reproductive success for year t (number of warblers fledged/number of warbler nesting
128 attempts/site), and site-specific cowbird reproductive success for year t (number of cowbirds
129 fledged/number of warbler nesting attempts/site) as potential explanatory variables. We controlled for the
130 seasonal decline in cowbird parasitism by including month of the nesting attempt (April-July) as a

131 continuous covariate in year $t+1$. In order to control for landscape-level effects of cowbird parasitism in
132 our analysis, where the site-specific parasitism rate was correlated among years because the configuration
133 of forest habitat and cowbird foraging areas remained nearly constant [43], we included the ambient
134 parasitism rate from the respective study site from year t (number of warbler nests parasitized/number of
135 warbler nesting attempts per site). Some studies have found variation in parasitism with respect to host
136 density [e.g. 44, 45]; therefore we included the site-specific warbler density (number of females/hectare in
137 year $t+1$) to investigate if a current condition such as the density of a quality host predicts the probability
138 of cowbird parasitism in year $t+1$.

139 Next, to elucidate whether site-wide cowbird success in year t positively correlates with the
140 probability of parasitism in both parasitized and non-parasitized nest boxes in year $t+1$, we used a subset
141 of data that included individual nest boxes used by warblers in consecutive years from non-manipulated
142 (i.e. without egg removal) study sites ($n = 245$). We included nesting attempts initiated in May of each
143 year to control for the seasonal decline in parasitism rates and matched individual nest boxes that were
144 used in two consecutive years. We included the parasitism status (categorical) and site-wide cowbird
145 success (continuous) in year t as explanatory variables and an interaction between the variables to predict
146 the parasitism probability for the same individual nest box in the following year ($t+1$).

147 **(c) Experimental cowbird egg removal**

148 We experimentally manipulated cowbird reproductive success by excluding predators and
149 removing cowbird eggs to reduce the potential confounds of environmental (e.g. water depth; [46]) and
150 host characteristics that may affect cowbird reproductive success and thus, potentially serve as cues for
151 cowbird egg-laying decisions. We placed nest boxes on two conduit poles with axle grease at least one
152 meter from the closet vegetation to eliminate nest predation and thus, maximize the likelihood of
153 cowbirds fledging from a parasitized nest. As part of other experimental studies, we removed all cowbird
154 eggs from approximately one-third of randomly selected candidate nest boxes. We compared the
155 likelihood of parasitism in year $t+1$ between two categories of parasitized nest boxes (in year t):
156 ‘removed’ nests ($n = 92$), where in the first year (t) all cowbird eggs were removed prior to a complete

157 clutch or during incubation (days 1-5) and, ‘fledged’ nests ($n = 188$), where at least one cowbird offspring
158 fledged in addition to warbler fledglings (in year t). Cowbird eggs removed from nests were collected for
159 future genetic analyses. The majority of ‘fledged’ nest boxes involved no cowbird egg removal, and
160 produced a single cowbird fledgling. Parasitized nest boxes which failed to fledge a cowbird due to,
161 predation, natural hatching failure or nestling death were not included in analyses. To control for potential
162 issues of non-independence, female warblers were only used once. We included the number of cowbird
163 eggs laid (continuous) and number of warblers fledging (continuous) in year t for each nest as a potential
164 explanatory variables of the parasitism probability the following year ($t+1$).

165 Next, we investigated the influence of cowbird and host reproductive output on the within-year
166 parasitism probability of subsequent breeding attempts, using a dataset that included only female warblers
167 that were parasitized during their successful first nest (initiated prior to 1 June) and then initiated a
168 subsequent attempt (i.e. double-brooding). We compared the probabilities of parasitism for second
169 breeding attempts between females that fledged any cowbird offspring ($n = 212$) and females that fledged
170 only warblers (where all cowbird eggs were removed) in their first attempt ($n = 100$). To control for
171 potential issues of non-independence, female warblers were only used once. We also controlled for the
172 number of cowbird eggs laid (continuous), number of warblers fledging (continuous), and the initiation
173 date of the second breeding attempt (ordinal date) when testing for an effect of egg removal (categorical
174 yes/no) on the parasitism status of second broods.

175 **(d) Statistical analyses**

176 We analyzed the probability of cowbird parasitism, a binary response variable, by using a series
177 of generalized linear mixed models (GLMMs) with Laplace approximation of the log likelihood [47] and
178 a logit link function (GLIMMIX; SAS 9.4; SAS Institute, Inc., Cary, NC, USA). We did not include
179 correlated explanatory variables ($r > 0.70$) in the same model to reduce any effects of collinearity among
180 variables. We included female warbler identity and study site and as a random effects in ‘study-site-
181 specific cowbird reproductive success models’ and included study site as a random effect in ‘experimental

182 cowbird egg removal' models. We presented model parameter estimates and associated standard errors (\pm
183 SE).

184 **RESULTS**

185 **(a) Study-site-specific cowbird reproductive success**

186 Of the 1458 warbler nests from non-manipulated study sites, 962 (66%) were parasitized by
187 brown-headed cowbirds. As expected, the rate of parasitism in year t ($\beta = 2.21$; $F_{1,851} = 12.36$; $p < 0.001$)
188 and month ($\beta = -1.51$; $F_{1,851} = 125.19$; $p < 0.001$) were positively correlated with probability of parasitism
189 in the following year ($t+1$). The probability of parasitism in year $t+1$ was positively influenced by
190 cowbird fledging success in year t ($\beta = 1.66$; $F_{1,851} = 5.71$; $p = 0.02$), increasing from 49% (± 0.10 SE)
191 when there was no cowbird fledging success to 72% (± 0.09 SE) when cowbird fledging success was at
192 its greatest observed levels in year t (0.6 cowbird fledged per warbler nesting attempt; Fig. 1).

193 Surprisingly, we found a relatively small ($\beta = -0.61$) but significant negative effect of site-specific warbler
194 reproductive output in year t on the probability of parasitism in year $t+1$ ($F_{1,851} = 16.42$; $p < 0.001$); where
195 sites that produced relatively few warblers per nesting attempt exhibited an increased likelihood of
196 parasitism the following year ($t+1$). This result may reflect a relationship between parasitism and egg
197 removal, as cowbirds often remove an egg prior to parasitism. We found no effect of female warbler
198 density in the current year on the parasitism rate for the current year ($\beta = 0.15$; $F_{1,851} = 1.03$; $p = 0.31$).

199 We then compared the influence of site-specific cowbird success on either parasitized or non-
200 parasitized nest boxes used in consecutive years on non-manipulated study sites using 245 nest boxes that
201 were initiated in May of each year. The probability of parasitism in year $t+1$ increased with increasing
202 site-specific cowbird reproductive success in year t ($\beta = 2.67$; $F_{1,56} = 4.66$; $p = 0.04$) (Fig.2). We found
203 that the probability of parasitism in year $t+1$ was significantly higher for those nests in year t that were
204 parasitized compared to those that were not (GLMM: $F_{1,56} = 5.85$; $p = 0.02$) (Fig. 2). There was no support
205 for an effect of the interaction between cowbird success and parasitism status on the likelihood of
206 parasitism between years ($F_{1,56} = 1.16$; $p = 0.29$).

207 **(b) Experimental cowbird egg removal**

208 Of the 280 parasitized nest boxes that successfully fledged any offspring (i.e. host or cowbird)
209 from experimental study sites in year t that were used by warblers in year $t+1$, we removed all cowbird
210 eggs from 92 nests. The removal of cowbird eggs explained variation among parasitism frequencies
211 between years (GLMM: $F_{1,258} = 8.05$; $p = 0.005$) where the probability of parasitism for nests that fledged
212 cowbirds (0.89 ± 0.03 SE) was greater than nests where cowbird eggs were removed (0.73 ± 0.06 SE; Fig.
213 3). The number of cowbird eggs laid ($\beta = 0.23$; $F_{1,258} = 1.85$; $p = 0.18$) and number of warblers fledged (β
214 $= 0.26$; $F_{1,258} = 3.23$; $p = 0.07$) from a nest box in year t were not correlated with likelihood of parasitism
215 the following year ($t+1$). The number of cowbird fledglings was negatively correlated with warbler
216 fledglings (Pearsons; $r = -0.52$; $p < 0.001$).

217 For the within-year analysis of the probability of parasitism during the second brood in relation to
218 cowbird success, we included 312 female warblers parasitized during their first broods that successfully
219 fledged any offspring (i.e. host or cowbird) and initiated an additional attempt (i.e. double-brooding). We
220 removed all cowbird eggs from 100 of these first broods. More than 90% of second clutches were
221 initiated within the same or adjacent nest box as the first brood. In a GLMM, controlling for the number
222 of cowbird eggs laid ($\beta = 0.25$; $F_{1,275} = 3.25$; $p = 0.07$), number of warblers fledged ($\beta = 0.10$; $F_{1,275} =$
223 1.05 ; $p = 0.31$), and the initiation date of the second brood ($\beta = -0.03$; $F_{1,275} = 3.68$; $p = 0.06$), the
224 probability of parasitism during the second brood for female warblers fledging ≥ 1 cowbird offspring
225 during their first breeding attempt (0.38 ± 0.06) was more than twice that of nests where we
226 experimentally removed all cowbird eggs (0.14 ± 0.05) ($F_{1,275} = 13.68$; $p = 0.002$; Fig. 4).

227 **DISCUSSION**

228 Our analyses revealed that brown-headed cowbirds increased their parasitism of prothonotary
229 warblers in response to past cowbird reproductive success both within and between years even after
230 controlling for confounding factors (site-specific parasitism rate and date) known to be important in our
231 study system. In particular, we detected a strong positive correlation between the site-specific cowbird
232 reproductive success one year and the likelihood of parasitism the following year for nest boxes that had

233 not previously been parasitized. Furthermore, our experimental removal of cowbird eggs decreased the
234 probability of parasitism for subsequent nesting attempts both within and between years.

235 Our results indicate that host use by female cowbirds is not merely a function of landscape
236 characteristics (e.g. fragmentation, edge effects), but also reflects the use of cowbird reproductive
237 performance information from past parasitism attempts. We also know from our long-term dataset and the
238 experimental data that cowbirds do not focus on particular female warblers or nest boxes, but rather
239 continue to update their selection of individual hosts based on the most current information. Furthermore,
240 we now know that cowbirds are not simply selecting hosts based on species-specific traits (e.g. song,
241 habitat, nest-site characteristics). We demonstrated that cowbirds can discriminate between areas of high
242 and low cowbird productivity within a single host species even while selecting amongst uniform nest sites
243 (i.e. nest boxes).

244 Female cowbirds may draw upon their own breeding experience (i.e. personal information) or
245 that of other cowbird females (i.e. social information), targeting productive locations and hosts to increase
246 their reproductive output. The use of personal and social information in breeding decisions has been
247 widely investigated in non-parasitic passerines [23, 48, 49], but this is the first example of experiential
248 information use documented within an obligate brood parasitic species. Lacking genetic data depicting the
249 egg-laying decisions for individual female cowbirds, we can only infer that females use personal, and
250 potentially social, information to enhance their reproductive potential. Because female cowbirds are often
251 faithful to an egg-laying area both within and between years [26, 30], our experimental removal of
252 cowbird eggs and resultant decrease in parasitism probability for subsequent breeding attempts within the
253 same nest box suggests that personal information is used to inform egg-laying decisions. The likelihood
254 of parasitism increased dramatically for non-parasitized nest boxes, in particular, when used again in the
255 year following a year with high site-wide cowbird success. This result may reflect site-faithful female
256 cowbirds increasing egg-laying in response to their own breeding experience and other female cowbirds
257 similarly responding to the cowbird productivity observed via prospecting.

258 Parasitism rates have been found to be positively correlated with host characteristics in some
259 systems, such as nest quality, body condition and social dominance [reviewed in 36, 37]. As many of
260 these host characters are sexually selected traits thought to serve as cues indicative of parental abilities,
261 brood parasites could potentially choose hosts based on trait conspicuousness or by collecting inadvertent
262 information (i.e. eavesdropping) if these host characters reflect the ability to successfully raise parasitic
263 offspring. Experimentally removing cowbird eggs from warbler nests, however, resulted in decreases in
264 parasitism probabilities on subsequent nesting attempts, thus reducing the confound of host traits being
265 correlated with host quality. Furthermore, previous studies from our system have shown that
266 morphological traits are not found to be correlated with parasitism rates for prothonotary warblers [35],
267 indicating that host traits are relatively unimportant influences on parasitism decisions within our study
268 population. Therefore, the apparent preference for host traits observed in other studies may reflect brood
269 parasites responding to success, rather than eavesdropping on heterospecific signals. One might expect
270 cowbirds generally to parasitize hosts that experience low rates of nest predation, indicated by high
271 fledging success of host young, particularly if cowbirds are able to assess that the presence of many host
272 fledglings on a site is a function of low rates of nest predation. Conversely, our results indicate that
273 warbler reproductive output is not a good predictor of cowbird parasitism in the subsequent nesting
274 attempt or between breeding seasons.

275 If juvenile cowbirds return to their natal location and/or host species to breed in subsequent years,
276 local recruitment of cowbird offspring on productive sites could account for the rise in parasitism between
277 years in response to cowbird reproductive success. Juveniles may preferentially parasitize the species that
278 raised them by imprinting on the host species itself [50, 51], on the nest characteristics of that species
279 [52], or on the habitat it was raised in [53]. As a cavity nesting passerine, the prothonotary warbler could
280 offer cowbirds a unique nestling experience and search image compared to other available species within
281 the host community. While many adult brood parasitic species exhibit breeding site fidelity [30, 54-56],
282 natal philopatry for cowbirds is considered uncommon [57]. Because cowbirds do not breed until ≥ 1 year
283 old [11], the effects of egg removal on parasitism rates between consecutive breeding attempts within a

284 given year (i.e. double-brooding) indicates that at the very least, adult female cowbirds use reproductive
285 performance information to guide within-year parasitism decisions. Therefore, the observed increase in
286 the probability of parasitism between years in response to cowbird reproductive success is more likely
287 explained by female breeding site fidelity rather than by the local recruitment of cowbird offspring alone.

288 Warbler density in the current year was examined as a potential predictor of cowbird parasitism
289 to investigate if female cowbirds parasitize warblers based on their abundance [e.g. 44, 45], instead of
290 their ability to fledge cowbird young. While we found no effect of warbler density in our study system,
291 the influence of host density on patterns of parasitism may vary depending on the host specificity of the
292 brood parasite and/or the quality of the host species parasitized [58]. The rate of cowbird parasitism for
293 prothonotary warblers could fluctuate in response to changes in the availability of alternative hosts, but
294 we did not measure changes in the densities or rates of cowbird parasitism of other hosts during the
295 course of this study. Nevertheless, it is difficult to imagine how the availability of alternative hosts in the
296 current year could fluctuate in parallel with cowbird reproductive success in a way that would undermine
297 the effect on cowbird parasitism of the warblers observed both within and between years.

298 In conclusion, our results suggest that the rate of parasitism for a high quality host was best
299 predicted by the brown-headed cowbird reproductive success of previous breeding attempts. This pattern
300 implies that cowbird females are monitoring their reproductive output to inform future breeding decisions,
301 thus providing a rare example of the influence of cognition on ecological and evolutionary processes in
302 natural populations [59]. Furthermore, investigating the use of social and/or personal information by
303 parasites has the potential to enhance our understanding of the evolution of host specificity and the effect
304 of parasite cognition on the development of anti-parasite defences in hosts.

305

306 **ETHICS**

307 This study was carried out in strict accordance with the recommendations in the Guidelines to the Use of
308 Wild Birds in Research (Available: <http://www.nmnh.si.edu/BIRDNET>). Research, including cowbird
309 egg collection and the colour-banding of warblers, was approved by the University of Illinois Institutional

310 Animal Care and Use Committee (Permit Numbers: 04092 and 10173), the U.S. Fish and Wildlife
311 Service (Permit Number: MB815400-0), and the U.S. Geological Survey (Banding Permit Number:
312 06507).

313

314 **DATA ACCESSIBILITY**

315 The datasets supporting this article are available at Dryad doi:10.5061/dryad.j04mk

316

317 **AUTHORS' CONTRIBUTIONS**

318 All authors contributed to the design of the study, collected field data and wrote the paper.

319

320 **ACKNOWLEDGEMENTS**

321 We thank V. Kichline, C. Buerke, C. Carreau, and J. York, for help collecting data and T.J. Benson for
322 assistance with statistical methodology. Our manuscript was greatly improved by the comments from A.
323 Suarez, R. Schooley and two anonymous reviewers. The staff from the Illinois Natural History Survey,
324 Cypress Creek National Wildlife Refuge and Cache River State Natural Area provided logistical support.

325

326 **REFERENCES**

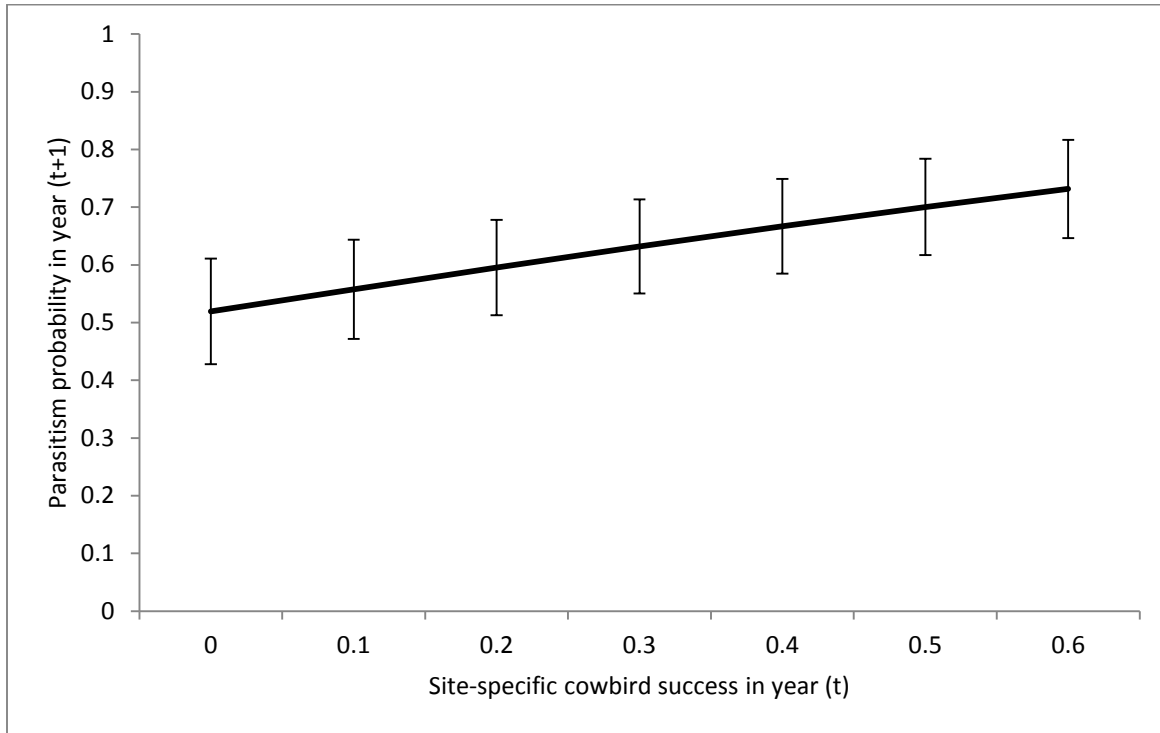
- 327 1. Rothstein SI. 1990 A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol.*
328 *Evol. Syst.* **21**, 481-508. (doi:10.1146/annurev.ecolsys.21.1.481)
- 329
- 330 2. Soler M. 2014 Long-term coevolution between avian brood parasites and their hosts. *Biol. Rev.*
331 **89**(3), 688-704. (doi:10.1111/brv.12075)
- 332
- 333 3. Feeney WE, Welbergen JA, Langmore NE. 2014 Advances in the study of coevolution between
334 avian brood parasites and their hosts. *Annu. Rev. Ecol. Evol. Syst.* **45**, 227-246. (doi:10.1146/annurev-
335 ecolsys-120213-091603)
- 336
- 337 4. Davies N.B. 2000 *Cuckoo, cowbirds and other cheats*. London, T. & A. Poyser; 310 p.
- 338
- 339 5. Kleven O, Moksnes A, Røskaft E, Honza M. 1999 Host species affects the growth rate of cuckoo
340 (*Cuculus canorus*) chicks. *Behav. Ecol. Sociobiol.* **47**(1-2), 41-46. (doi:10.1007/s002650050647)
- 341
- 342 6. Soler JJ, Møller AP, Soler M. 1999 A comparative study of host selection in the European cuckoo
343 *Cuculus canorus*. *Oecologia* **118**(2), 265-276. (doi:10.1007/s004420050727)

- 344
345 7. De Mársico MC, Reboreda JC. 2008 Differential reproductive success favours strong host
346 preference in a highly specialized brood parasite. *Proc.R. Soc. B* **275**(1650), 2499-2506.
347 (doi:10.1098/rspb.2008.0700)
348
- 349 8. Grim T, Samas P, Moskat C, Kleven O, Honza M, Moksnes A, Roskaft E, Stokke BG. 2011
350 Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? *J. Anim.*
351 *Ecol.* **80**(3), 508-518. (doi:10.1111/j.1365-2656.2010.01798.x)
352
- 353 9. Davies N, Brooke MdL. 1989 An experimental study of co-evolution between the cuckoo,
354 *Cuculus canorus*, and its hosts. I. Host egg discrimination. *J. Anim. Ecol.* **58**(1)207-224.
355 (doi:10.2307/4995)
356
- 357 10. Rothstein SI, Patten MA, Fleischer R.C. 2002 Phylogeny, specialization, and brood parasite—
358 host coevolution: some possible pitfalls of parsimony. *Behav. Ecol.* **13**(1), 1-10.
359 (doi:10.1093/beheco/13.1.1)
360
- 361 11. Lowther PE. 1993 Brown-headed cowbird (*Molothrus ater*). In *The Birds of North America* (ed.
362 Poole A., Gill, F.). Ithaca, Cornell Lab of Ornithology.
363
- 364 12. Ortega CP. 1998 *Cowbirds and other brood parasites*, University of Arizona Press; i-xvii, 1-371
365 p.
366
- 367 13. Briskie J, Sealy S, Hobson K. 1990 Differential parasitism of least flycatchers and yellow
368 warblers by the brown-headed cowbird. *Behav. Ecol. Sociobiol.* **27**(6), 403-410.
369 (doi:10.1007/bf00164066)
370
- 371 14. Curson DR, Goguen CB, Mathews NE. 2010 Community-level patterns of population recruitment
372 in a generalist avian brood parasite, the brown-headed cowbird. *Oecologia* **163**(3), 601-612.
373 (doi:10.1007/s00442-010-1630-4)
374
- 375 15. Feeney WE, Langmore NE. 2013 Social learning of a brood parasite by its host. *Biol. Lett.* **9**(4),
376 20130443. (doi:10.1098/rsbl.2013.0443)
377
- 378 16. Molina-Morales M., Martínez J.G., Martín-Gálvez D., Dawson D.A., Burke T., Avilés J.M. 2014
379 Cuckoo hosts shift from accepting to rejecting parasitic eggs across their lifetime. *Evolution* **68**(10), 3020-
380 3029. (doi:10.1111/evo.12471)
381
- 382 17. Thorogood R, Davies NB. 2013 Reed warbler hosts fine-tune their defenses to track three decades
383 of cuckoo decline. *Evolution* **67**(12), 3545-3555. (doi:10.1111/evo.12213)
384
- 385 18. Campobello D, Sealy SG. 2011 Use of social over personal information enhances nest defense
386 against avian brood parasitism. *Behav. Ecol.* **22**(2), 422-428. (doi:10.1093/beheco/arq225)
387
- 388 19. Middleton ALA. 1977 Effect of cowbird parasitism on american goldfinch nesting. *Auk* **94**(2),
389 304-307.
390
- 391 20. Pöysä H. 2003 Parasitic common goldeneye (*Bucephala clangula*) females lay preferentially in
392 safe neighbourhoods. *Behav. Ecol. Sociobiol.* **54**, 30-35. (doi:10.1007/s00265-003-0596-1)
393

- 394 21. Pöysä H. 2006 Public information and conspecific nest parasitism in goldeneyes: targeting safe
395 nests by parasites. *Behav. Ecol.* **17**, 459-465. (doi:10.1093/beheco/arj049)
396
- 397 22. Avilés JM, Stokke BG, Parejo D. 2006 Relationship between nest predation suffered by hosts and
398 brown-headed cowbird parasitism: a comparative study. *Evol. Ecol.* **20**, 97-111. (doi:10.1007/s10682-
399 005-4989-7)
400
- 401 23. Danchin É, Giraldeau LA, Valone TJ, Wagner RH. 2004 Public information: from nosy
402 neighbors to cultural evolution. *Science* **305**, 487-491. (doi:10.1126/science.1098254)
403
- 404 24. Schmidt KA, Dall SRX, Van Gils JA. 2010 The ecology of information: an overview on the
405 ecological significance of making informed decisions. *Oikos* **119**, 304-316. (doi:10.1111/j.1600-
406 0706.2009.17573.x)
407
- 408 25. Alderson GW, Gibbs HL, Sealy SG. 1999 Determining the reproductive behaviour of individual
409 brown-headed cowbirds using microsatellite DNA markers. *Anim. Behav.* **58**, 895-905.
410 (doi:10.1006/anbe.1999.1220)
411
- 412 26. Hahn DC, Sedgwick JA, Painter IS, Casna NJ. 1999 A spatial and genetic analysis of cowbird
413 host selection. In *Research and management of the brown-headed cowbird in western landscapes* (eds.
414 Morrison M.L., Hall L.S., Robinson S.K., Rothstein S.I., Hahn D.C., Rich T.D.), pp. 204-217.
415
- 416 27. Strausberger BM, Ashley MV. 2005 Host use strategies of individual female brown-headed
417 cowbirds *Molothrus ater* in a diverse avian community. *J. Avian Biol.* **36**, 313-321. (doi:10.1111/j.0908-
418 8857.2005.03323.x)
419
- 420 28. McLaren C, Woolfenden B, Gibbs H, Sealy S. 2003 Genetic and temporal patterns of multiple
421 parasitism by brown-headed cowbirds (*Molothrus ater*) on song sparrows (*Melospiza melodia*). *Can. J.*
422 *Zool.* **81**, 281-286. (doi:10.1139/z03-002)
423
- 424 29. Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use
425 by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187-193. (doi:10.1016/j.tree.2005.01.010)
426
- 427 30. Dufty AM. 1982 Movements and activities of radio-tracked brown-headed cowbirds. *Auk* **99**,
428 316-327.
429
- 430 31. Sherry DF, Forbes MR, Khurgel M, Ivy GO. 1993 Females have a larger hippocampus than
431 males in the brood-parasitic brown-headed cowbird. *Proc. Natl. Acad. Sci. U.S.A.* **90**, 7839-7843.
432 (doi:10.1073/pnas.90.16.7839)
433
- 434 32. Guigueno MF, Snow DA, MacDougall-Shackleton SA, Sherry DF. 2014 Female cowbirds have
435 more accurate spatial memory than males. *Biol. Lett.* **10**, 20140026. (doi:10.1098/rsbl.2014.0026)
436
- 437 33. Hoover JP, Robinson SK. 2007 Retaliatory mafia behavior by a parasitic cowbird favors host
438 acceptance of parasitic eggs. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 4479-4483.
439 (doi:10.1073/pnas.0609710104)
440
- 441 34. Hauber ME, Yeh PJ, Roberts JO. 2004 Patterns and coevolutionary consequences of repeated
442 brood parasitism. *Proc. R. Soc. B* **271**, S317-S320. (doi:10.1098/rsbl.2004.0168)
443

- 444 35. Hoover JP, Yasukawa K, Hauber ME. 2006 Spatially and temporally structured avian brood
445 parasitism affects the fitness benefits of hosts' rejection strategies. *Anim. Behav.* **72**, 881-890.
446 (doi:10.1016/j.anbehav.2006.02.011)
447
- 448 36. Parejo D, Avilés J. 2007 Do avian brood parasites eavesdrop on heterospecific sexual signals
449 revealing host quality? A review of the evidence. *Anim. Cogn.* **10**, 81-88. (doi:10.1007/s10071-006-0055-
450 2)
- 451 37. Feeney WE, Welbergen JA, Langmore NE. 2012 The frontline of avian brood parasite–host
452 coevolution. *Anim. Behav.* **84**, 3-12. (doi:10.1016/j.anbehav.2012.04.011)
453
- 454 38. Petit LJ. 1999 Prothonotary warbler, *Prothonotaria citrea*. In *The Birds of North America* (ed.
455 Poole A., Gill, F.). Philadelphia.
- 456
- 457 39. Hoover JP. 2003 Experiments and observations of prothonotary warblers indicate a lack of
458 adaptive responses to brood parasitism. *Anim. Behav.* **65**, 935-944. (doi:10.1006/anbe.2003.2154)
459
- 460 40. Hoover JP, Reetz MJ. 2006 Brood parasitism increases provisioning rate, and reduces offspring
461 recruitment and adult return rates, in a cowbird host. *Oecologia* **149**, 165-173. (doi:10.1007/s00442-006-
462 0424-1)
- 463
- 464 41. Hoover J.P. 2003 Multiple effects of brood parasitism reduce the reproductive success of
465 prothonotary warblers, *Protonotaria citrea*. *Anim. Behav.* **65**, 923-934. (doi:10.1006/anbe.2003.2155)
466
- 467 42. Louder MIM, Schelsky WM, Benson TJ, Hoover JP. 2015 Brown-headed cowbirds exploit a
468 host's compensatory behavioral response to fecundity reduction. *Behav. Ecol.* **26**, 255-261.
469 (doi:10.1093/beheco/aru187)
470
- 471 43. Hoover JP, Hauber ME. 2007 Individual patterns of habitat and nest-site use by hosts promote
472 transgenerational transmission of avian brood parasitism status. *J. Anim. Ecol.* **76**, 1208-1214.
473 (doi:10.1111/j.1365-2656.2007.01291.x)
474
- 475 44. Woolfenden BE, Gibbs HL, McLaren CM, Sealy SG. 2004 Community-level patterns of
476 parasitism: use of three common hosts by a brood parasitic bird, the brown-headed cowbird. *Ecoscience*
477 **11**, 238-248. (doi:10.1525/auk.2009.09053)
478
- 479 45. Stokke BG, Hafstad I, Rudolfson G, Bargain B, Beier J, Campas D.B, Dyrz A, Honza M, Leisler
480 B, Pap PL, et al. 2007 Host density predicts presence of cuckoo parasitism in reed warblers. *Oikos* **116**,
481 913-922. (doi:10.1111/j.2007.0030-1299.15832.x)
482
- 483 46. Hoover JP. 2006 Water depth influences nest predation for a wetland-dependent bird in
484 fragmented bottomland forests. *Biol. Conserv.* **127**, 37-45. (doi:10.1016/j.biocon.2005.07.017)
485
- 486 47. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009
487 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127-
488 135. (doi:10.1016/j.tree.2008.10.008)
489
- 490 48. Doligez B, Danchin E, Clobert J. 2002 Public information and breeding habitat selection in a wild
491 bird population. *Science* **297**, 1168-1170. (doi:10.1126/science.1072838)
492
- 493 49. Hoover JP. 2003 Decision rules for site fidelity in a migratory bird, the prothonotary warbler.
494 *Ecology* **84**, 416-430. (doi:10.1890/0012-9658(2003)084[0416:DRFSFI]2.0.CO;2)

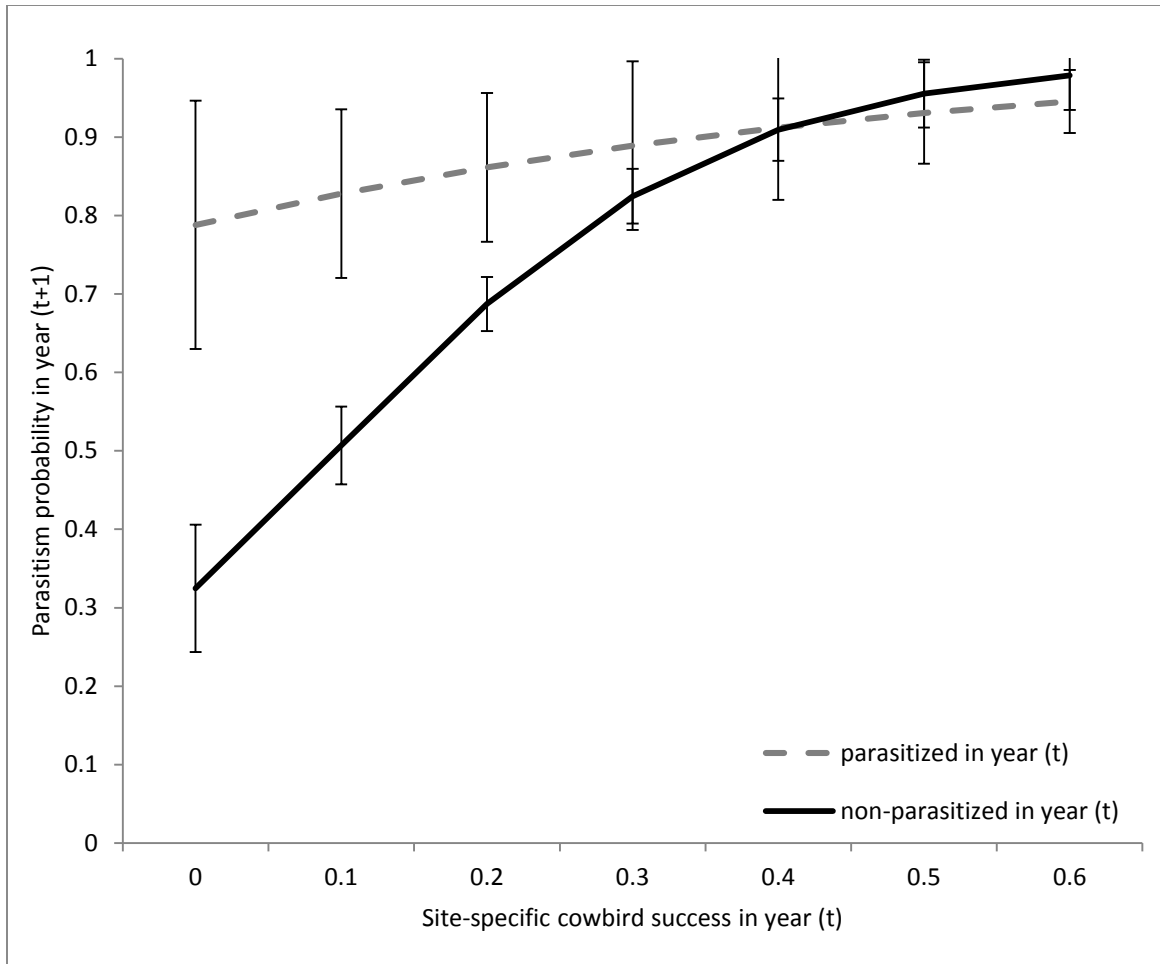
495
496 50. Ellison K, Sealy S, Gibbs H. 2006 Genetic elucidation of host use by individual sympatric
497 bronzed cowbirds (*Molothrus aeneus*) and brown-headed cowbirds (*M. ater*). *Can. J. Zool.* **84**, 1269-
498 1280. (doi:10.1139/z06-091)
499
500 51. Payne RB, Payne LL, Woods JL, Sorenson MD. 2000 Imprinting and the origin of parasite-host
501 species associations in brood-parasitic indigobirds, *Vidua chalybeata*. *Anim. Behav.* **59**, 69-81.
502 (doi:10.1006/anbe.1999.1283)
503
504 52. Mahler B, Confalonieri VA., Lovette IJ, Reboreda JC. 2007 Partial host fidelity in nest selection
505 by the shiny cowbird (*Molothrus bonariensis*), a highly generalist avian brood parasite. *J. Evol. Biol.* **20**,
506 1918-1923. (doi:10.1111/j.1420-9101.2007.01373.x)
507
508 53. Teuschl Y, Taborsky B, Taborsky M. 1998 How do cuckoos find their hosts? The role of habitat
509 imprinting. *Anim. Behav.* **56**, 1425-1433. (doi:10.1006/anbe.1998.0931)
510
511 54. Soler JJ, Soler M, Møller AP, Martinez JG. 1995 Does the great spotted cuckoo choose magpie
512 hosts according to their parenting ability? *Behav. Ecol. Sociobiol.* **36**, 201-206. (doi:10.1007/bf00177797)
513
514 55. Raim A. 2000 Spatial patterns of breeding female brown-headed cowbirds on an Illinois site. In
515 *Ecology and management of cowbirds and their hosts: studies in the conservation of North American*
516 *passerine birds*. (eds. Smith J.N.M., Cook T.L., Rothstein S.I., Robinson S.K., Sealy S.G.), pp. 87-99,
517 University of Texas Press.
518
519 56. Langmore NE, Adcock GJ, Kilner RM. 2007 The spatial organization and mating system of
520 Horsfield's bronze-cuckoos, *Chalcites basalis*. *Anim. Behav.* **74**, 403-412.
521 (doi:10.1016/j.anbehav.2006.09.019)
522
523 57. Hauber ME, Strausberger BM, Feldheim KA, Lock J, Cassey P. 2012 Indirect estimates of
524 breeding and natal philopatry in an obligate avian brood parasite. *J. Ornithol.* **153**, 467-475.
525 (doi:10.1007/s10336-011-0762-6)
526
527 58. Jensen WE, Cully JF. 2005 Density-dependent habitat selection by brown-headed cowbirds
528 (*Molothrus ater*) in tallgrass prairie. *Oecologia* **142**, 136-149. (doi:10.1007/s00442-004-1709-x)
529
530 59. Morand-Ferron J, Cole EF, Quinn JL. 2015. Studying the evolutionary ecology of cognition in the
531 wild: a review of practical and conceptual challenges. *Biol Reviews*. (doi:10.1111/brv.12174)
532



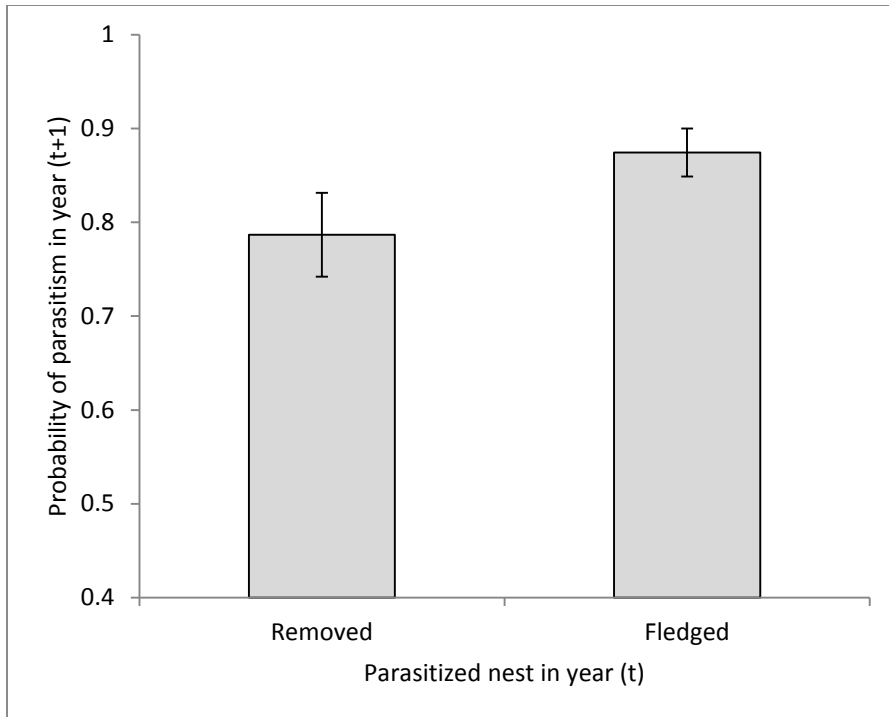
534

535 Figure 1. The relationship between the site-specific cowbird reproductive success in year t and the
536 probability of parasitism for nests within that given study site the following year ($t+1$). Results of a
537 GLMM ($n = 1458$ nests) and the mean predicted probability of parasitism (\pm SE) are presented while
538 holding additional explanatory variables at mean observed values; data includes nests from non-
539 manipulated study sites (i.e. without egg removal) and both study site and female warbler identity were
540 included as a random effects.

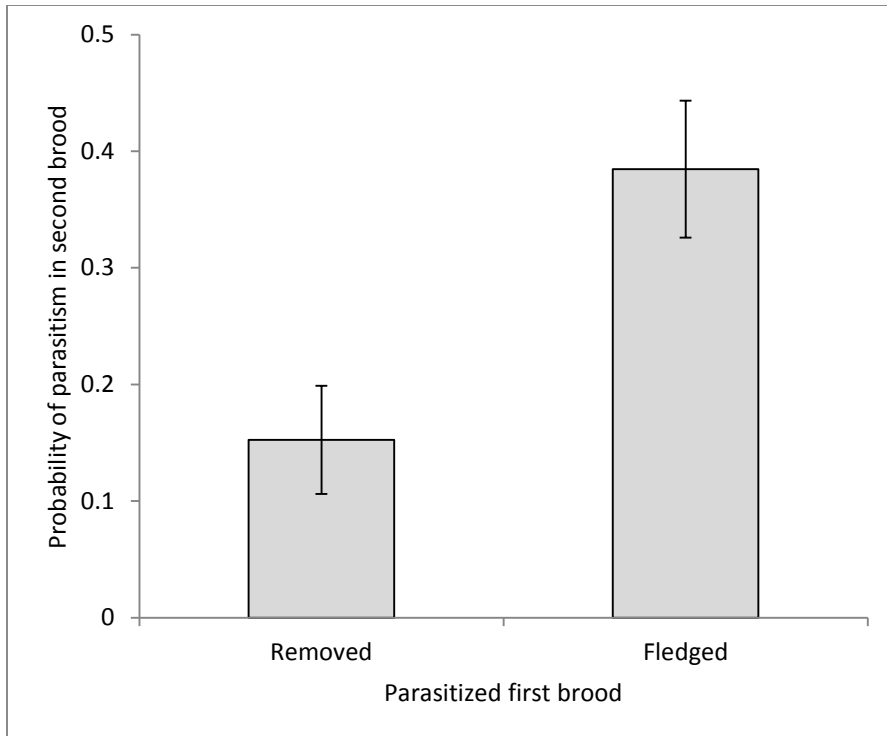
541



542
 543 Figure 2. The comparison between the site-specific cowbird reproductive success in year t and the
 544 probability of parasitism the following year ($t+1$) for nest boxes used by warblers in consecutive years;
 545 nest boxes parasitized (gray dotted line) in year t and non-parasitized (black line) in year t . Results of a
 546 GLMM ($n = 245$ nests) and the mean predicted probability of parasitism (\pm SE) are presented while
 547 holding additional explanatory variables at mean observed values; data includes nests from non-
 548 manipulated study sites (i.e. without egg removal) and both study site and female warbler identity were
 549 included as a random effects.
 550



551
552 Figure 3. The comparison between parasitized nests where all cowbird eggs were removed versus nests
553 where ≥ 1 cowbird offspring fledged in year t and the probability of parasitism the following year ($t+1$)
554 for nest boxes used by warblers in consecutive years. Results of a GLMM ($n = 280$ nests) and the mean
555 predicted probability of parasitism (\pm SE) are presented while holding additional explanatory variables at
556 mean observed values; study site included as a random effect.
557
558
559
560



561
562 Figure 4. The relationship between parasitized first broods where all cowbird eggs were removed versus
563 nests where ≥ 1 cowbird offspring fledged and the probability of parasitism for the second brood (i.e.
564 double-brooding). Results of a GLMM ($n = 312$ nests) and the mean predicted probability of parasitism
565 (\pm SE) are presented while holding additional explanatory variables at mean observed values; study site
566 included as a random effect.
567

