

1 **Indiscriminate aggression and threat-level insensitive egg rejection maintain**
2 **host susceptibility towards sexually dimorphic diderik cuckoos**

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11 **Abstract**

12

13 The existence of adult sexual dimorphism is typically explained as a consequence of sexual
14 selection, yet coevolutionary drivers of sexual dimorphism frequently remain untested. Here, I
15 investigate the role of sexual dimorphism in host-parasite interactions of the brood parasitic
16 diederik cuckoo, *Chrysococcyx caprius*. Female diederik cuckoos are more cryptic in appearance
17 and pose a threat to the clutch, while male diederik cuckoos are conspicuous and not a direct
18 threat. Specifically, I examine whether sexual dimorphism in diederik cuckoos provokes threat-
19 level sensitive responses in Southern red bishop, *Euplectes orix*, hosts. I use experimentally
20 simulated nest intrusions to test whether hosts have the capacity to differentially (i) detect, and/or
21 (ii) discriminate between, male and female diederik cuckoos, relative to harmless controls.
22 Overall, I found no evidence that diederik cuckoos differ in detectability, since both sexes are
23 comparable to harmless controls in the probability and speed of host detection. Furthermore,
24 neither male nor female hosts discriminate between sexually dimorphic diederik cuckoos when
25 engaging in frontline nest defences. However, hosts that witnessed a male diederik cuckoo during
26 the trial were more than twice as likely to reject odd eggs compared to those that saw a control.
27 Moreover, hosts were more likely to reject experimental eggs when exposed to a male compared
28 to a female diederik cuckoo: the reverse of a beneficial threat-level sensitive response. While the
29 cryptic appearance of female diederik cuckoos does not differentially avoid detection by hosts, it
30 does appear to provide the benefit of anonymity given the egg rejection costs of male-like
31 appearance in the nest vicinity. These findings have implications for the evolution and
32 maintenance of sexual dimorphism across the Cuculidae, and highlight the value of testing
33 assumptions about the ecological drivers of sexual dimorphism.

34

35 **Keywords:** sexual dimorphism, discrimination, brood parasitism, coevolution, Cuculidae.

36 **Introduction**

37 Sex differences in adult phenotypes are widely considered to arise as a consequence of
38 dissimilar selection acting on the sexes (Darwin, 1871; Andersson, 1994; Parker, et al., 1972;
39 Mank, 2008). While evidence supports the role of sexual selection as an underlying driver of
40 sexually dimorphic phenotypes in many cases, the contribution of natural selection frequently
41 remains untested, despite evidence that multiple selective pressures can contribute to the origin
42 and maintenance of sex-specific adult phenotypes (Shine, 1989; Owens & Hartley, 1998;
43 Székely, et al., 2000; Law & Mehta, 2018). Consequently, it is valuable to examine the ecological
44 drivers and adaptive value of sex-linked traits, since numerous assumptions and hypotheses
45 remain untested (Shine, 1989; Runemark et al., 2018).

46 Brood parasitic cuckoos (Cuculidae) provide an interesting test case in the evolution of
47 adult sex differences for three main reasons. First, brood parasitic cuckoos do not invest effort in
48 rearing young, and thus differential selection in mating success due to the costs, constraints or
49 genetic architecture underlying the expression of parental care are absent in both the males and
50 females of these species (Payne, 1967; Trivers, 1972; Krüger, 2007; Kokko & Jennions, 2008;
51 Royle, Smiseth, Kölliker, 2012). Second, because paternal contributions to care do not influence
52 male fitness and it is derived exclusively via mating success, sexual selection on traits that
53 influence the number of fertilisations achieved by males could be intensified. However,
54 comparative analyses of sexual dimorphism in brood parasitic cuckoos show that it is not driven
55 by sexual selection, which typically selects for larger body size in males (Krüger et al., 2007).
56 Furthermore, female brood parasitic cuckoos lay numerous eggs (up to 21 eggs produced in 10
57 weeks; Davies, 2000; Payne, 2005) which, when compared with species characterised by small
58 clutch size and/or single broods, means that in relative terms, fertilisation opportunities are not
59 rare for either sex. While these factors do not completely exclude sexual selection from shaping
60 adult cuckoo phenotypes in some way, the magnitude of effect could differ substantially from
61 other species, and from previous assumptions (Mokos et al., 2021). Third, traits that facilitate the
62 brood parasitic behaviour of females are crucial, since these characteristics play a central role in
63 the successful insertion of an egg into the host clutch, and hence, all ensuing fitness outcomes.
64 Indeed, comparative analyses show that sexual dimorphism arises via female-biased phenotypic
65 change (Krüger et al., 2007). Crucially, across the Cuculidae, the brood parasitic cuckoo females
66 are more cryptic than males and crypsis is considered important in avoiding detection by the
67 hosts of brood parasitic species (Payne, 1967; Krüger et al., 2007). Yet, whether hosts
68 differentially detect or discriminate between adult brood parasitic cuckoos on the basis of sex
69 differences in characteristics has rarely been investigated (York & Davies, 2017). This is

70 important because identifying brood parasitic threats can provide hosts with the opportunity to
71 mount behavioural defences such as aggressive mobbing and egg rejection, which can be costly
72 and/or fatal for cuckoos, and are key mechanisms for coevolutionary consequences for adult
73 brood parasitic cuckoo phenotypes (Davies, 2000; York, 2021).

74 Here, I test whether host defences against brood parasitism differ according to sex
75 differences in adult diderik cuckoo (*Chrysococcyx caprius*) appearance using a model
76 presentation experiment at the nests of free-living hosts. Diederik cuckoos are sexually dimorphic
77 in plumage and facial colouration, with females presenting a more cryptic adult phenotype than
78 conspicuous males (Figure 1; Reed, 1968; Rowan, 1983; Payne, 2005). Indeed, the onomatopoeic
79 common name “diederik” itself arises from the distinctive whistling ‘*dee dee dee dee-derik*’ call
80 of the male, and which is broadcast loudly and frequently during the breeding season (Reed,
81 1968). They are obligate, host-evicting brood parasites with a number of host species among the
82 Ploceidae (the weaverbirds; Rowan, 1983; Payne, 2005). One species that is regarded a
83 particularly frequent host is the Southern red bishop (*Euplectes orix*), but surprisingly little is
84 known about the ecological and evolutionary dynamics between Southern red bishops and
85 diderik cuckoos (Reed, 1968; Rowan, 1983; Lawes & Kirkman, 1996). Southern red bishops are
86 a polygynous and colonial weaverbird species that occurs widely across sub-Saharan Africa
87 (Friedl & Klump, 1999; Friedl, 2004; Metz, Klump, & Friedl, 2009). In wetland habitat, male
88 Southern red bishops defend small (~ 3 m across) breeding territories where they build numerous
89 nests to attract females (Metz, Klump, & Friedl, 2009). Upon selecting a nest, the female bishop
90 lays her eggs, then incubates and provides care for offspring, which can include a brood parasitic
91 diderik cuckoo chick. Brood parasitism incidence varies widely and ranges from 0 — 67% of
92 nests across colonies at different sites and between years (Hunter, 1961; Payne & Payne, 1967;
93 Jensen & Vernon, 1970; Rowan, 1983).

94 Specifically, I examine whether the sexual dimorphism of male and female diderik
95 cuckoos provokes threat-level sensitive responses in a common host species, the Southern red
96 bishop, *Euplectes orix*. First, I test the hypothesis that female diderik cuckoo cryptic appearance
97 has evolved due to the benefits of being less detectable to hosts. Using simulated intrusions of
98 male and female diderik cuckoo at the host nest, I test whether males and females differ in
99 detectability (probability and speed) by their hosts, relative to harmless controls (dark-capped
100 bulbuls, *Pycnonotus tricolor*). Given the evidence that, across species, brood parasitic females are
101 more cryptic (Payne, 1967; Reed, 1968; Krüger et al., 2007), I predict that female diderik
102 cuckoos are less easily detected by hosts, and therefore hosts should be less likely to respond, or
103 take longer to respond, to females compared to more conspicuous males and controls. Second, I

104 used simulated nest intrusions to test whether hosts can discriminate between males and females
105 by exhibiting differences in defences (frontline aggression and egg rejection) toward the male (no
106 threat) compared to the female (high threat). The capacity to adjust behavioural defences towards
107 intruders according to the scale of the threat they pose is observed among some species of
108 weaverbirds (York, Wells & Young, 2019). Moreover, weaverbird hosts are aggressive toward
109 diederik cuckoo, and while they will readily strike diederik cuckoo mounts, they produce milder
110 aggression toward other species of cuckoo that do not target weaverbirds as their hosts, which
111 suggests an underlying capacity to discriminate between heterospecifics in accordance with the
112 threat they present (Rowan, 1983; Noble, 1995; Lawes & Kirkman, 1996). I predict that if hosts
113 discriminate they benefit from directing greater aggression and stronger egg rejection defences
114 toward the greater brood parasitic threat of female diederik cuckoos. Finally, given that host
115 populations are heterogeneous in terms of the defences that brood parasites experience on
116 approaching a nest, I examine the role of intraspecific variation in host responses to intrusions at
117 the nest. In particular, I examine whether male and female hosts differ in their responses to the
118 simulated intrusions. I predict that male hosts will be more aggressive toward the intruding threat
119 than females because males build and defend nest structures, so they are likely to be more
120 vigilant and aggressive toward intruders in the nest vicinity.

121

122 **Materials and Methods**

123 *General methods*

124 I conducted fieldwork between October 2019 and March 2020 and collected data for this
125 experiment from a population of diederik cuckoo and Southern red bishops on private wetlands in
126 Gauteng, South Africa, where I have been observing and studying these species since circa 2017.
127 Diederik cuckoos are intra-African breeding migrants and they arrive in the highveld region from
128 the first weeks of October onwards, with peak laying activity in December (Reed, 1968). Each
129 year, breeding males build multiple nests on small territories to attract matings with females
130 (Figure 1 shows a section of reed bed). Nests were monitored from construction through laying
131 and incubation using individual markers on a supporting reed stem. Nest locations and placement
132 were monitored and male movements between nests were observed with binoculars. Diederik
133 cuckoo were heard calling and displaying throughout the study period. Interspecific brood
134 parasitism was assessed by observing egg size and appearance and whether a pencil mark
135 adhered to the shell (Lawes & Kirkman, 1996; Lindholm, 1997). Natural brood parasitism
136 incidence in this population during the study period occurred in 7 — 20% (87 monitored to clutch
137 completion) of nests, with 7% matching diederik cuckoo egg characteristics and 20% including

138 potential intra-specific brood parasitism (Lawes & Kirkman, 1996; Lindholm, 1997). These
139 estimates were not confirmed with nestling characteristics in the majority of cases. Natural brood
140 parasitism events are brief and challenging to study, and all data presented here use the
141 experimental approach described below.

142

143 *Experimental design*

144 I conducted an independent-measures paired-design experiment with 72 host subjects at
145 36 nests between December 2019 and January 2020 on days when weather conditions were dry
146 and wind levels were low. At each nest, I simulated brood parasitism with a foreign egg by
147 selecting one egg at random from the clutch and painting it with Mont Marte acrylic ‘titanium’
148 white, dotted at random with ‘burnt umber’ brown spots (following previously validated
149 methods: Davies & Brooke, 1988; Thorogood & Davies, 2016; York & Davies, 2017), before
150 returning the egg to the nest. This approach facilitates studies of egg rejection by hole ejectors
151 (they peck a small hole in the shell to grip the egg and eject it from the nest) and eggs that are not
152 rejected by the host will subsequently hatch (Thorogood & Davies, 2016; York & Davies, 2017).
153 I used a heavily maculated non-mimetic egg appearance similar to the Southern masked weaver
154 (*Ploceus velatus*) because (1) this pattern is similar to the eggs laid by some diderik cuckoo at
155 this site and cuckoos will occasionally lay in the nest of non-preferred hosts (Davies, 2000), (2)
156 this host species is not highly discriminating towards model eggs during egg laying or after clutch
157 completion, but will reject heavily maculated or greatly mis-matched model eggs across this
158 period (Lawes & Kirkman, 1996), and (3) rejection rates in this population were previously
159 unknown, so a non-mimetic egg ensured interpretable data regardless of how discriminating hosts
160 were against egg appearance. Following the brood parasitism simulation, I then positioned an
161 adult bird model (details below) on the outside of the nest at the lip of the entrance hole and
162 positioned a video camera (Panasonic HC-V270EB-K HD) on a tripod at 5 m from the focal nest,
163 before retreating to observe the focal nest with binoculars from a distance of at least 20 m. After
164 the trial was complete, I returned to collect the camera and remove the model. In all cases, hosts
165 were observed in the reeds surrounding the focal nest area during the experimental trial.

166 The model type presented at each nest was pre-determined using latin square to allocate
167 the treatments through the course of the experiment, and an independent measures design was
168 used to avoid carry-over effects of model presentations, since these can elicit intense behavioural
169 responses and lasting physiological effects which may influence subsequent behavioural
170 responses to stimuli (Apfelbeck, Stegherr & Goymann, 2011). This design also facilitated
171 measurement of egg rejection responses through simulated brood parasitism, which can only be

172 carried out once per nest after exposure to adult heterospecific model stimuli. Nests were
173 sufficiently separated (at least 10 m from the nearest neighbouring experimental territory, and
174 therefore separated by territories between) to avoid model presentations at one nest influencing
175 responses at another. Territories were not selected in the most central region of the reed bed to
176 mitigate positional effects on host responsiveness that could conceivably arise through nesting
177 density (Ferguson, 1994; Lawes & Kirkman, 1996). Simulated intrusions were carried out during
178 the late morning or afternoon, when natural brood parasitism attempts are more likely to occur
179 (Chance, 1940; Lindholm, 1997). Nest contents were checked at one day and three days after the
180 trial to record rejection or acceptance of experimental eggs. Methodology received ethical
181 clearance from the University of Cambridge (ZOO69/19) and the University of Pretoria
182 (NAS197), and fieldwork was conducted under permit.

183

184 *Model bird stimuli*

185 Adult bird models were printed three-dimensionally in plastic and painted to match the
186 appearance of the focal species. Such models provoke equivalent behavioural responses to
187 taxidermy mounts and live birds, and are readily reproducible. I presented three model treatments
188 (n = 12 nests per treatment group) with one treatment type per nest: male diederik cuckoo, female
189 diederik cuckoo, and harmless dark-capped bulbul control, by alternating between two identical
190 model exemplars of each treatment type. I selected dark-capped bulbuls as a harmless control for
191 four reasons: (1) they are a similar body size to diederik cuckoo (19 - 20 cm in length) which
192 controls for size effects on detectability, (2) dark-capped bulbuls are abundant at this study site,
193 which mitigates issues of neophobic responses to novel stimuli, (3) bulbuls present no ecological
194 threat to Southern red bishops since they are neither predatory nor are they niche competitors,
195 and (4) their plumage includes both inconspicuous (drab brown and off-white) and conspicuous
196 (bright yellow vent) colouration, which provides scope to draw contrast with the more
197 conspicuous male diederik cuckoos to interpret responses in the context of model detectability
198 versus model identity. None of the models were finished with iridescent colouration to
199 standardise the model design, and because the iridescence of diederik cuckoos does not show
200 strongly in the light environment where their hosts nest (Reed, 1968).

201

202 *Behavioural responses*

203 To investigate Southern red bishop behavioural responses to model stimuli, data were
204 collected from both male and female individuals at each nest. Male and female Southern red
205 bishops are conspicuously dimorphic in plumage colouration during the breeding season. During

206 the experimental period (December — January) all males were in full breeding plumage, with
207 bright red and black colouration, which ensured ease of discriminating them from female (brown
208 and streaky) hosts. Female southern red bishops can also be differentiated from other locally
209 occurring weaverbird species using relative size, plumage and body shape characteristics, and
210 they occur infrequently in the nest vicinity. Host behavioural responses were extracted from the
211 video files (as below). These responses were selected as proxies for (1) model detection (the
212 probability and latency to approach the nest vicinity, and the probability and latency to approach
213 the model), and (2) discrimination between models (the probability and latency to attack the
214 model and the probability of egg rejection). Trials commenced on placement of the model and
215 video camera at the nest, and were observed from a distance of at least 20 m using binoculars.
216 Hosts were confirmed to be present in the nest area during the trial in all cases. Because this host
217 species nests colonially, aggressive responses by the focal hosts can also elicit mobbing
218 behaviour from neighbouring males and females. The behavioural responses selected for analysis
219 in this study use the initial behavioural state change (i.e. host presence, approach, strike).
220 Response intensity was not considered here, but descriptions of front line defence intensity
221 toward the model are provided in the Results.

222 Egg rejection responses were assessed at one day, and again after three days, since the
223 model presentation trial, because cuckoo egg rejections typically occur during the first day, and
224 relatively few occur after three days, and because excess nest visits can increase predation risk or
225 clutch abandonment (Reed, 1968; Brooke & Davies, 1988). Responses were recorded for the
226 presence (acceptance = 1) or absence (rejection = 0) of the experimental egg in the nest by
227 examining the contents. Nests were checked for signs of depredation and in one case, nest
228 contents were depredated at day one (the nest and supporting reeds were destroyed from below).
229 In three cases, the nest contents could not be checked on day one, and in four cases contents were
230 checked on day four or five instead of day three, due to logistical constraints. These data are
231 coded as missing values (NA), since data were not collected at the specified time point (Table 2
232 and 3). Findings do not differ if the non-standard observations are considered.

233 234 *Video analysis*

235 Behavioural responses during the trial period were recorded on video at 50 frames per
236 second, at a resolution of 1,920 x 1,080, with the framing and zoom view for each nest specified
237 using the ‘grid’ function and saved as MPEG-4 video files. The following behavioural event data
238 were extracted for male and female Southern red bishops during the 5 min trial from the videos
239 with VLC (VideoLan) using x0.25 playback speed to determine the following event timing of the

240 behavioural response to the second: (i) entering the nest vicinity, where the focal bird was in a
241 similar plane to the model (gauged by relative body size); (ii) approaching the model, where the
242 focal bird was less than two model lengths (approximately 40 cm, within the supporting or
243 adjacent reeds to the nest) away from the model, and had moved towards the model; (iii) first
244 physical contact with the model: ‘strike’, using the beak or feet.

245 For both male and female hosts, these raw data were then used to calculate the latencies
246 (in seconds) to: (1) entering the nest vicinity; (2) approaching the model; (3) attacking the model.
247 All three variables were extracted for the first male and first female to enter the frame. In a
248 minority of cases, additional neighbouring males and females later entered the frame to
249 contribute to collective mobbing attacks on the model (see Results). I also calculated the lag
250 (seconds) between the time point at which individual hosts that enter the nest vicinity then
251 subsequently approached the model. This ‘approach window’ was used to investigate whether the
252 window of time between initially detecting the model (entering the vicinity) and responding to
253 the model (approaching the model) differed across the three treatments, since rapid responses on
254 detecting stimuli are associated with aggression (Apfelbeck, Stegherr & Goymann, 2011) and
255 could be a selective pressure on cuckoo laying speed (Chance, 1940). Example video file
256 [embedded media link].

257

258 *Statistical analyses*

259 Data supporting the following analyses are available (dryad doi: __). All analyses were
260 conducted in R (version 4.2.3; R Development Core Team, 2015) by fitting models with all terms
261 of interest (the full model) and determining the significance of each explanatory variable by
262 removing the term from the full model to test for a change in deviance in the fit of the model
263 without that specific term (Forstmeier & Schielzeth, 2011). Linear mixed effects models (LMM,
264 package ‘lme4’; Bates, Maechler, & Bolker, 2014) and generalised linear mixed-effects models
265 (GLMM) were inspected for over-dispersion, zero-inflation, normality and heteroscedasticity, as
266 appropriate, and were satisfactory unless otherwise stated (R package ‘DHARMA’; Hartig 2022).
267 The details for each analysis are provided below.

268

269 *Frontline aggression responses*

270 To analyse the probability of hosts to respond to the simulated intrusion at their nest, I
271 used a GLMM with binomial error (logit-link function for each binary response term: Table 1 a-
272 c). In each case, the fixed terms ‘treatment’ (‘bulbul’/‘male diderik’/‘female diderik’), host sex
273 (male/ female), and the interaction between ‘treatment’ x ‘host sex’, were specified in the full

274 model, as was the random term ‘nest ID’ to control for paired responses by male and female host
275 parents from the same focal nest. To investigate whether the ‘approach window’ of time between
276 initially detecting the model (entering the vicinity) and responding to the model (approaching the
277 model) differed across the three treatments, I used an LMM with a gaussian distribution. Again,
278 the fixed terms ‘treatment’ (‘bulbul’/‘male diderik’/‘female diderik’), host sex (male/female),
279 the interaction between ‘treatment’ x ‘host sex’, and the random term ‘nest ID’ were specified in
280 the full model. The response variable ‘approach window’ was square-root transformed prior to
281 analysis for normality of residuals.

282 To analyse the latencies of aggression responses of hosts subjected to a simulated
283 intrusion at their nest, I used an analytical approach designed for censored data. In this
284 experiment, all response latencies were capped at the end of the simulated intrusion trial, which
285 was standardised to five minutes. In the majority of cases, the responses occurred within the trial
286 period, but where the behavioural event did not occur within the trial period, the response was
287 allocated the maximum value of the trial duration (300 seconds). Consequently, for these
288 censored data (the absolute value is constrained by the sampling approach) where the relative
289 position of the data point is nevertheless informative (e.g. yet to respond at five minutes after the
290 trial had begun), can be captured in the analysis. Mixed-effects survival models (MESM) with
291 Cox proportional hazards (Therneau, 2015; package ‘coxme’) were used because, in addition to
292 being designed for censored data, they also permit random terms to be fitted, in this case, to
293 control for multiple data points from the same focal nest. One model was fitted for each response
294 term: (1) ‘latency to enter nest vicinity’; (2) ‘latency to approach the model’; and (3) ‘latency to
295 attack the model’. In all cases, the fixed terms ‘treatment’ (‘bulbul’/‘male diderik’/‘female
296 diderik’), host sex (male/female), the interaction between ‘treatment’ x ‘host sex’, and the
297 random term ‘nest ID’ were specified in the full model.

298

299 *Experimental brood parasitism egg rejection responses*

300 For analyses of the probability of experimental egg rejection of hosts, I used generalized
301 linear models (GLM) with binomial error (logit-link function) for each binary response term
302 (Table 2 and Table 3). In each case, the fixed terms ‘treatment’ (‘bulbul’/‘male diderik’/‘female
303 diderik’), whether or not the focal host male or female individual entered the nest vicinity during
304 the trial (‘in vicinity’, yes/no), and the interaction between ‘treatment’ x ‘in vicinity’, were
305 specified in the full model. The term ‘in vicinity’ was included because the sight of a cuckoo at
306 the nest is known to increase the probability of hosts rejecting experimental eggs (Davies &
307 Brooke, 1989; Thorogood & Davies, 2016). Because individual-level egg rejection response data

308 for each male and female host was not feasible to collect for this study (in contrast to individual-
309 level data on whether the host observed the model at the nest, see above), and because it was not
310 deemed justified to assume that either the male or the female host is solely responsible for egg
311 rejection decisions, a dataset was analysed for each host sex: ‘male host in vicinity during trial’
312 (Table 2) and ‘female host in vicinity during trial’ (Table 3), and separate analyses for each
313 dataset are presented. Significant interaction terms were further examined by comparing the
314 model with all three levels with a simpler model where the two levels for the contrast of interest
315 were collapsed to test for a change in deviance in the fit of the model (i.e with or without the
316 level of interest).

317

318 **Results**

319 Southern red bishop male and female (n = 72) responses during simulated heterospecific
320 intrusion trials at host nests (n = 36) were qualitatively similar to those described for taxidermy
321 mounts (Rowan, 1983; Noble, 1995) and natural interactions (pers. obs.) in other contexts.
322 During all trials I observed through binoculars at a distance whether hosts were near the nest (< 2
323 m), and in each case this was confirmed.

324

325 *(1) Do male or female Southern red bishop hosts differentially detect diderik cuckoos at the nest*
326 *due to sex differences in appearance?*

327 The majority of hosts (over 83%) entered the nest vicinity during the five minute model
328 presentation. Over sixty percent of hosts entered the nest vicinity and subsequently approached
329 the model within approximately 40 cm (i.e. within striking range) during the trial period.
330 Analyses of individual host responses to simulated intrusions at the nest revealed that the proxies
331 for *detection* (entering the nest vicinity and approaching the nest) were similar across the three
332 treatments. Treatment type did not have a significant effect on host probability (GLMM: $\chi^2 =$
333 0.12, P = 0.94) and latency (MESM: $\chi^2 = 0.30$, P = 0.86) to *enter the nest vicinity* (Table 1a;
334 Figure 2 a-b), neither did host sex (probability: $\chi^2 = 1.35$, P = 0.24; latency: $\chi^2 = 1.84$, P = 0.17,
335 Figure 3 a-b), or the interaction between treatment type and host sex (probability: $\chi^2 = 1.44$, P =
336 0.49; latency: $\chi^2 = 0.33$, P = 0.85). Similarly, treatment type did not have a significant effect on
337 host probability (GLMM: $\chi^2 = 0.68$, P = 0.71) or latency (MESM: $\chi^2 = 0.14$, P = 0.93) to
338 *approach the model* (Table 1b; Figure 2 c-d), and again neither did host sex (probability: $\chi^2 =$
339 0.31, P = 0.58; latency: $\chi^2 = 0.72$, P = 0.40; Figure 3 c-d), or the interaction between host sex and
340 treatment (probability: $\chi^2 = 3.04$, P = 0.22; latency: $\chi^2 = 2.64$, P = 0.27). To examine the

341 possibility that host speed of approach varied according to treatment type, I also calculated the
342 'approach window' (lag in seconds between the time point at which hosts that did enter the nest
343 vicinity then approached the model). There was also no significant effect of treatment on the
344 approach window (LMM: $\chi^2 = 1.33$, $P = 0.51$, $n = 44$ of 72 individuals; bulbul: $n = 13$; male
345 diederik: $n = 16$; female diederik: $n = 15$), or the interaction between treatment and host sex ($\chi^2 =$
346 0.53 , $P = 0.77$), or host sex ($\chi^2 = 2.32$, $P = 0.13$). But in general, females that enter the nest
347 vicinity ($n = 21$) consistently approach more rapidly (mean \pm SE: 12.9 ± 4.41 seconds) than
348 males ($n = 23$, mean \pm SE: 49.4 ± 16.3 seconds), presumably due to a stereotyped approach route
349 to the nest during early incubation, while males typically move comprehensively through their
350 nesting territory.

351

352 *(2) Do male or female Southern red bishop hosts discriminate between male and female diederik*
353 *cuckoo according to the direct threat-level they pose to offspring?*

354 While the vast majority of hosts approached the model during the trial (75% of those that
355 enter the nest vicinity), a smaller proportion (24% of individuals that approach the model)
356 physically attacked the model by striking it with their beaks and/or feet. Where attacks on the
357 model did occur, they were typically forceful and in some cases dislodged the model from the
358 nest entrance, despite it being firmly attached to the supporting reeds. Occasionally, intense
359 attacks (at a rate of 17 strikes per min) recruited contributions from neighbouring males in the
360 colony. Due to the relative infrequency of such collective mobbing responses, it is not currently
361 possible to make inferences about factors that contribute to their occurrence. That said, collective
362 mobbing responses were evenly distributed across the three treatments, so there is currently no
363 indication that collective responses arise due to model discrimination. Indeed, analyses of
364 individual behavioural responses revealed no significant effect of treatment type on attack
365 probability (GLMM: $\chi^2 = 0.01$, $P = 0.99$, Table 1c) or latency to attack (MESM: $\chi^2 = 0.054$, $P =$
366 0.97 , Figure 2 e-f), and no significant effect of an interaction between treatment type and host sex
367 (probability: $\chi^2 = 0.13$, $P = 0.94$, Table 1c; latency: $\chi^2 = 2.47$, $P = 0.29$), despite a significant
368 effect of host sex on both the probability ($\chi^2 = 22.78$, $P < 0.001$, Table 1c) and the latency ($\chi^2 =$
369 7.35 , $P = 0.0067$, Figure 3 e-f) to attack the model. This effect is driven by male hosts carrying
370 out the vast majority of attacks on the model, with females engaging less than half as frequently
371 as males, and taking longer on average where they did attack the model. Because female hosts
372 attack rarely and exclusively attack when the male host engages in attacking, large variance is

373 attributed to 'nest ID'. Absolute estimates from this model should be treated with caution due to
374 zero-inflation that arises from attacks being rare (Figure 2e).

375 Egg rejection responses were largely similar after one day (GLM: $\chi^2 = 7.03$, $P = 0.030$)
376 and three days (GLM: $\chi^2 = 6.76$, $P = 0.034$) since the trial, revealing a significant interaction
377 between treatment type and whether the male host was in the nest vicinity during the trial (Table
378 2 and 3, Figure 4). In several cases where the nests were over dry ground, the experimental egg
379 was found below the nest with a small hole pecked in the shell due to host rejection of the egg.
380 When hosts are not in the nest vicinity during the trial, they are equally likely to accept or reject
381 experimental eggs in each treatment group. Contrasts to probe which treatment levels contribute
382 to the significant interactions are provided below to aid with interpretation.

383 We do not yet know whether male or female hosts are responsible for egg rejection
384 decisions in Southern red bishops. Male hosts entered the nest vicinity during over 80% of trials,
385 while female hosts were 5% less likely than males to enter the nest vicinity during the trial. When
386 a male host was in the nest vicinity during the trial, hosts rejected two thirds as many
387 experimental eggs when exposed to a male diderik cuckoo (day 1: 60% rejected; GLM: $\chi^2 =$
388 7.56, $P = 0.023$; day 3: 67% rejected; $\chi^2 = 6.87$, $P = 0.032$; Table 2; Figure 4 a-b) compared to a
389 bulbul control (day 1 - 3: 18 - 27% rejected). Whereas when male hosts observe a female diderik
390 model on their nest, hosts do not differentially reject experimental eggs (day 1: 36% rejected, $\chi^2 =$
391 1.01, $P = 0.60$; day 3: 45% rejected, $\chi^2 = 0.91$, $P = 0.64$) when contrasted with bulbul controls.
392 However, hosts reject marginally more experimental eggs when male hosts observe a male
393 diderik cuckoo compared to a female diderik cuckoo on the nest ($\chi^2 = 4.73$, $P = 0.094$), but this
394 effect does not persist after three days post-trial ($\chi^2 = 4.53$, $P = 0.10$). When the female host was
395 in the vicinity during the trial, a similar pattern arises (Table 3; Figure 4 c-d). Hosts have a
396 marginally higher probability of rejecting experimental eggs when a female host observes a male
397 diderik cuckoo compared to a bulbul control model on the nest (day 1: $\chi^2 = 4.78$, $P = 0.092$; day
398 3: $\chi^2 = 4.79$, $P = 0.091$). Conversely, hosts do not differentially reject experimental eggs when
399 exposed to a female diderik model in contrast with bulbul controls (day 1: $\chi^2 = 0.62$, $P = 0.73$;
400 day 3: $\chi^2 = 2.28$, $P = 0.32$). When female hosts observe a male diderik cuckoo on the nest,
401 hosts do not reject significantly more eggs after one day than when they observe a female
402 diderik cuckoo on the nest ($\chi^2 = 3.99$, $P = 0.14$), but after three days, hosts have rejected
403 significantly more experimental eggs when exposed to a male compared to a female diderik
404 cuckoo on the nest ($\chi^2 = 8.99$, $P = 0.011$).

405 **Discussion**

406 Sexual dimorphism in brood parasitic diederik cuckoos most likely evolved due to
407 benefits in coevolutionary interactions with their weaverbird hosts, and the findings presented
408 here suggest that host perceptual processing likely plays a key role in the mechanisms of
409 selection on adult cuckoo phenotypes. Across cuckoos, brood parasitic females are more cryptic
410 than males, yet the benefit of cryptic plumage, in diederik cuckoos at least, is not clearly linked to
411 the benefits of avoiding detection by hosts, since there is no evidence that Southern red bishop
412 hosts differentially detect heterospecifics at the nest. Despite the fact that the vast majority of
413 hosts (over 83%) entered the nest vicinity and subsequently closely approached the model, the
414 likelihood and speed at which hosts approached the model was near identical across treatment
415 groups. However, female diederik cuckoos may nevertheless benefit from the relative anonymity
416 that their appearance bestows compared to the more conspicuous appearance of male diederik
417 cuckoos, since Southern red bishop hosts differentially reject experimental eggs when they
418 observe a male diederik cuckoo at the nest. This finding is the complete opposite of predictions if
419 hosts discriminate between male and female diederik cuckoo on the basis of their brood
420 parasitism threat-level, which would allow hosts to perform responses adjusted to the sex-specific
421 level of the threat. Furthermore, Southern red bishop hosts were indiscriminately aggressive
422 toward simulated heterospecific intruders at the nest. Together, these findings suggest that,
423 despite Southern red bishop hosts having the capacity to mount frontline mobbing and egg
424 rejection defences, they remain vulnerable to brood parasitism by diederik cuckoos because it is
425 challenging for them to correctly identify and respond appropriately to the threat.

426 Why are Southern red bishop hosts more likely to reject eggs when exposed to a male
427 diederik cuckoo model on their nest? This pattern was the opposite of predictions, given that the
428 female diederik cuckoo was the only treatment that presents a direct brood parasitism threat. This
429 finding does not arise because females are less detectable (Figure 2a), or because hosts are less
430 likely to approach closely enough to have the opportunity to identify salient features of female
431 diederik cuckoos (Figure 2c). Instead, differential rejection responses could be explained by the
432 high stimulus valence or salience of a male diederik cuckoo at the nest. One component of male
433 diederik cuckoo appearance that could be particularly salient to hosts is their red iris and eye-ring
434 (Figure 1). While this may seem a relatively small component of diederik cuckoo overall
435 appearance, avian eyes can be highly salient and important mediators of inter-specific
436 interactions (Trnka, Prokop & Grim, 2012; Davidson et al., 2014; Davidson et al., 2017).
437 Furthermore, Southern red bishops make use of red colouration as a dominant component in their
438 breeding plumage and their sensitivity to detecting and processing red signals is central to

439 reproduction, therefore likely consequences of ‘sensory drive’ due to sensory biases from sexual
440 signalling of hosts could explain their overall stronger rejection responses to witnessing a male
441 diderik cuckoo at the nest (Endler, 1992; Endler & Basolo, 1998). Given host egg rejection
442 responses when faced with a male diderik cuckoo, it is certainly beneficial for female diderik
443 cuckoos to be relatively anonymous, and it is notable that they lack a conspicuous red iris and
444 eye-ring (Reed, 1968). Indeed, simulated female diderik cuckoo nest intrusions provoke egg
445 rejection responses to a similar extent as a harmless bulbul. While further examination of
446 Southern red bishop perception would be necessary to confirm that diderik cuckoo red stimuli
447 are sufficient to drive behavioural responses, it is relevant to note that the bulbul models included
448 a conspicuous bright yellow patch, and so it is unlikely that my findings are driven simply by
449 conspicuousness.

450 Could host responses to male diderik cuckoos be advantageous for brood parasitism? If
451 male diderik cuckoo red iris and eye-ring colouration provide adaptive benefits for diderik
452 cuckoo due to hosts finding male diderik cuckoos salient, this could arise via sensory
453 exploitation (a perceptual mechanism more frequently invoked in the evolution of sexual
454 signalling; Ryan, 1990). Hosts could conceivably develop a misdirected learned association
455 between the more conspicuous male diderik cuckoo appearance and a threat to nest contents.
456 Indeed, hosts are frequently exposed to male diderik cuckoos, because male diderik cuckoos
457 are particularly conspicuous in the local area when the males are pursuing matings with
458 inconspicuous and secretive females (Reed, 1968; Lindholm, 1997). Therefore, hosts likely do
459 have sufficient opportunity to learn associations between male diderik cuckoos and either
460 general nest threats, or brood parasitism specifically, and such information could also become
461 socially transmitted by observing conspecifics mobbing diderik cuckoos. Social learning is
462 implicated in similar systems such as the more frequently studied reed warbler and common
463 cuckoos (Thorogood & Davies, 2016). One possible selective benefit of male diderik cuckoo
464 appearance tapping into the perceptual biases of Southern red bishops is that hosts could direct
465 their mobbing efforts towards the more apparent threat of the male diderik cuckoo, which in
466 turn, could generate or facilitate opportunities for secretive and rapid laying visits by females.
467 Consistent with this hypothesis, there are reports that suggest male diderik cuckoos assist
468 ovipositing females by distracting hosts (Jensen & Jensen, 1969). Similar team tactics and ‘luring
469 behaviours’ are documented in other species of cuckoos (Davies, 2000). However, I found no
470 evidence that Southern red bishop hosts were more likely to attack, or attacked male diderik
471 cuckoos more rapidly, compared to the other heterospecific intruders. Moreover, even if hosts are
472 distracted with the task of aggressively repelling a male diderik cuckoo, thereby facilitating a

473 window of opportunity for a stealthy female diderik cuckoo to lay undetected, those hosts that
474 have observed a male diderik cuckoo in the nest vicinity are more likely to reject odd eggs in the
475 clutch. That said, it is conceivable that host egg rejection responses to observing a male diderik
476 cuckoo in the nest vicinity could occur *because of* host counter-adaptations or learned responses
477 against male-facilitated host-luring tactics. Crucially, although it seems intuitive that hosts in an
478 aggressive state provoked by the male diderik's red eye colouration (potentially due to sensory
479 bias consequences of host sexual signalling) subsequently reject odd eggs, there was no evidence
480 that hosts were more aggressive when exposed to male diderik cuckoo compared to other
481 heterospecific intruders. Interestingly, across brood parasite hosts, frontline aggression and egg
482 rejection responses rarely correlate, suggesting that frontline behaviours (i.e. aggressive or wary
483 responses) do not predict egg rejection decisions (Thorogood & Davies, 2016; York & Davies,
484 2017). Hosts may simultaneously find the red eye-ring salient and this may influence rejection
485 decisions, while overt aggressive responses are variable across hosts. Regardless of the exact
486 mechanism or stage in coevolutionary dynamics, given the findings presented here, diderik
487 cuckoos would benefit from males avoiding close proximity to Southern red bishop nests,
488 especially when female cuckoos are laying, and in particular from having females that do not
489 look like males.

490 Other than the effect of host sex (host males are more aggressive than females; Figure 3e-
491 f), it is not yet clear what underlies aggressive response thresholds in Southern red bishops.
492 Southern red bishops are polygynous and males dominate aggressive responses toward nest
493 intruders. Their threshold for engaging in an attack is probably relatively high since they have
494 numerous nests to defend, and there are economic and temporal trade-offs in attacks against
495 conspecific and heterospecific intruders (Metz, Klump, & Friedl, 2009; Edler et al., 2011). For
496 example, male Southern red bishops also spend considerable time and effort in nest construction
497 and courtship display to attract multiple mates, and nest defence likely trades-off against these
498 important tasks, meaning that male attention towards detecting threats could be diluted (Metz,
499 Klump, & Friedl, 2009; Edler et al., 2011). Whether or not Southern red bishop aggressive
500 defences toward heterospecifics at their nests involve only generalised nest defences, or whether
501 they possess diderik cuckoo specific defences was not examined here, but it seems unlikely
502 given the indiscriminate aggression towards all simulated heterospecific intruder categories
503 (Duckworth, 1991). Further work to investigate how nesting density and colony size affect
504 aggression thresholds and collective defence in Southern red bishop would be helpful for
505 estimating population level variation in aggressive defence to which diderik cuckoos are
506 exposed (Ferguson, 1994; Lawes & Kirkman, 1996).

507 The variation in the aggressive behaviour of Southern red bishop hosts towards
508 heterospecific intruders in this population has implications for coevolutionary interactions and the
509 evolution of sexual dimorphism in diederik cuckoos. First, a larger proportion of hosts were wary
510 of the models and, despite approaching the model and looking directly at the model, did not then
511 engage in an aggressive response. This highlights that diederik cuckoos may frequently avoid the
512 direct costs of physical aggression from Southern red bishop hosts, along with avoiding the wider
513 issue of increased vigilance by neighbours alerted to brood parasitism risk (as observed in other
514 brood parasite systems) and as a consequence of population heterogeneity in host aggressiveness
515 (Campobello & Sealy, 2018). Second, diederik cuckoos do not appear to be disadvantaged by
516 lacking overt hawk-like appearance or plumage characteristics (York, 2021). That said, despite
517 lacking prominent chest-barring, diederik cuckoos do exhibit underwing barring that can be
518 concealed or revealed flexibly, so further investigation is now required to determine whether host
519 aggression toward diederik cuckoos is modulated by this potentially hawk-like characteristic
520 (Lyon & Gilbert, 2013; York, 2021). Finally, it is perhaps surprising that hosts were not
521 consistently aggressive toward diederik cuckoos, given their reputation for fierce attacks upon
522 diederik cuckoo near the colony (Rowan, 1983). However, it is important to recognise that such
523 attacks are eye-catching and even keen observers are unlikely to document instances where
524 cuckoos are not attacked by hosts, underlining the necessity for carefully designed experiments.

525 Both the indiscriminate aggression toward heterospecifics, and the likely trade-off
526 between aggression and other reproductive behaviours by males, together mean that rapid laying
527 speed is a particularly effective adaptation for diederik cuckoos since they might go undetected
528 while a male Southern red bishop is otherwise engaged (Metz, Klump, & Friedl, 2009; Edler et
529 al., 2011). Selection on laying speed is likely relatively strong since female cuckoos lay in less
530 than ten seconds (Chance, 1940; Lindholm, 1997; Payne, 2005), and because in this study for
531 over 80% of cases, models were observed by at least one host at short range during a five minute
532 experimental window, with more than half of hosts reaching close proximity to the nest within
533 two to three minutes of model placement. These findings highlight that an information-gathering
534 function (Chance, 1940) of triggering host mobbing near active nests (either to find nest locations
535 through conspicuous mobbing calls, or to identify ‘good’ hosts that are aggressive toward
536 intruders) is unlikely to be effective here. Hosts infrequently engage in mobbing, which coupled
537 with the physical costs when aggression does occur, mean that it is likely more beneficial for
538 diederik cuckoos to gather information on hosts away from the vicinity of the nest and, when
539 ready to lay, to visit nests rapidly. However, because Southern red bishop clutches are small
540 (mode 3 eggs), when female diederiks attempt to lay in dense colonies it could pose a

541 considerable challenge to get the timing right. Furthermore, atypically for passerines,
542 weaverbirds such as Southern red bishops begin egg laying before the nest is complete, and as a
543 consequence, the eggs are visible through the weave of the nest (Davies, 2000). This fact could
544 explain why, despite the potential costs of visiting nests, female diederik cuckoos may benefit
545 from approaching nests closely since, when coupled with dense colonies with limited vantage
546 points, it may be more challenging for her to monitor the brief laying window from afar. It is
547 therefore conceivable that if the ancestral state was for both male and female diederik cuckoo to
548 exhibit showy red facial colouration, that there would be selective advantage for female diederik
549 facial colouration to become less showy, especially if the female must inspect nests closely when
550 laying. This sequence is supported by comparative analyses that reconstruct the most likely
551 evolutionary pathway for sexual dimorphism in cuckoos involving a transition from showy to
552 cryptic (Kruger et al., 2007).

553 There are several implications from these findings for the evolution and maintenance of
554 sexual dimorphism in diederik cuckoos and across the Cuculidae: (i) they provide new evidence
555 that sexual dimorphism in brood parasitic cuckoos has evolved and/or is maintained due to
556 benefits in coevolutionary interactions with hosts, (ii) while females are more cryptic and males
557 are more conspicuous, there was no difference in how detectable or how likely hosts were to
558 approach male or female diederik cuckoos at the nest. This does not mean that the more cryptic
559 appearance of females is not beneficial in reducing detection in all contexts (e.g. females may
560 avoid harassment while monitoring host nests from afar), but it may play a less important role
561 than the effect of being relatively anonymous and less salient to hosts when in the nest vicinity;
562 (iii) if the effects observed here are due to counter-adaptations or learned responses to
563 misdirection of host attention (via sensory exploitation with male red iris and eye ring
564 colouration), we might expect to find host-specific effects in other host weaverbird species that
565 lack red colouration. In these cases, other diederik cuckoo traits and behaviours might be more
566 important, which would be consistent with the existence of host-specific *gentes* that occur in
567 diederik cuckoo but are less well investigated than for other cuckoo species (Reed, 1968; Jensen
568 & Vernon, 1970; Martinez et al., 1998); (iv) it is worth noting that, while red eye-ring and iris
569 colouration is unique among the African members of the genus *Chrysococcyx*, red facial
570 colouration does occur in close relatives such as the Asian *C. xanthorhynchus* and *C. maculatus*,
571 Australian *C. minutillus*, and elsewhere in the Cuculidae (e.g. parental Malkohas where both
572 sexes exhibit showy red facial colouration, and more extensively than their brood parasitic male
573 relatives); (v) it remains possible that showy traits in male brood parasitic cuckoos could be
574 beneficial in coevolutionary interactions with hosts, or could even be *synergistic* with the

575 evolution of cryptic or anonymous traits associated with female phenotypes. Finally, given that in
576 some species of brood parasitic cuckoos facial colouration occurs as distinct sex-specific morphs
577 (diederik cuckoo), and in other species female polymorphisms have benefits in brood parasitic
578 interactions with hosts (common cuckoo), the role of host perception and defences against brood
579 parasites may be much more important than sexual selection in the evolution of sex-specific
580 morphs within this group (Kruger, et al., 2007; Thorogood & Davies, 2012; Mank, 2023).
581 Nonetheless, there is some evidence of multifunctional behavioural signalling in adult brood
582 parasitic cuckoos (Moskát & Hauber, 2019), and so future research on the role of sexual selection
583 in the evolution of adult cuckoo phenotypes will aid a complete understanding of these complex
584 and multimodal suites of traits.

585

586 **Conclusions**

587 The results presented here demonstrate that cryptic female diederik cuckoos are not
588 afforded reduced detection at the nest when compared with more conspicuous heterospecific
589 intruders. However, hosts are more likely to reject experimental eggs after viewing a conspicuous
590 male diederik cuckoo than a similarly conspicuous harmless dark-capped bulbul control.
591 Consequently, host perceptual processes may explain why diederik cuckoo sexual dimorphism is
592 characterised by a more anonymous female and a male with specific conspicuous characteristics,
593 but further investigation is needed to determine which features provoke host responses.
594 Combined together, the indiscriminate aggression and threat-level insensitive egg rejection of
595 Southern red bishop hosts maintains their susceptibility to brood parasitism, and furthermore,
596 indicate important factors and pathways that may underlie the origin and maintenance of sexual
597 dimorphism in diederik cuckoo, and more broadly across the Cuculidae.

598

599 **References**

- 600 Andersson, M. (1994) *Sexual selection*, Princeton University Press.
- 601 Apfelbeck, B., Stegherr, J. & Goymann, W. (2011) Simulating winning in the wild – the
602 behavioural and hormonal response of black redstarts to single and repeated territorial
603 challenges of high and low intensity. *Hormones and Behaviour*, 60: 565-571.
- 604 Bates, D., Maechler, M., & Bolker, B. (2014) lme4: linear mixed-effects models using Eigen and
605 Eigenpack. *Journal of Statistical Software*, 65: 1-68.
- 606 Campobello, D., and Sealy, S.G. (2018) Evolutionary significance of anti-parasite, anti-
607 predator and learning phenotypes of avian nest defence. *Scientific Reports* 8: 1-10.
- 607 Chance, E.P. (1940) *The Truth About the Cuckoo* (Country Life, London).
- 608 Darwin, C. *Sexual selection and the descent of man*. London: Murray, 1871.

609 Davidson, G.L., Clayton, N.S. and Thornton, A. (2014). Salient eyes deter conspecific nest
610 intruders in wild jackdaws (*Corvus monedula*). *Biology Letters* 10: 20131077.

611 Davidson, G.L., Thornton, A. and Clayton, N.S. (2017). Evolution of iris colour in relation to
612 cavity nesting and parental care in passerine birds. *Biology Letters* **13**:
613 20160783.20160783.

614 Davies, N.B. & Brooke, M. de L. (1988) Cuckoos versus reed warblers: adaptations and counter-
615 adaptations. *Animal Behaviour* 36, 262–28.

616 Davies, N.B. & Brooke, M. de L. (1989) An experimental study of co-evolution between the
617 cuckoo *Cuculus canorus* and its hosts. 1. Host discrimination. *Journal of Animal Ecology*
618 58, 207–224.

619 Davies, N.B. (2000) *Cuckoos, cowbirds and other cheats*. London, UK: Poyser.

620 Duckworth, J.W. (1991) Responses of breeding reed warblers *Acrocephalus scirpaceus* to
621 mounts of sparrowhawk *Accipiter nisus*, cuckoo *Cuculus Canorus* and jay *Garrulus*
622 *glandarius*. *Ibis* 133: 68-74.

623 Edler, R., Goyman, W., Schwabl, I., and Friedl, T.W.P. (2011) Experimentally elevated
624 testosterone levels enhance courtship behaviour and territoriality but depress acquired
625 immune response in Red Bishops *Euplectes orix*. *Ibis* 153: 46-58.

626 Endler, J.A. (1992). Signals, signal conditions, and the direction of evolution. *The American*
627 *Naturalist* 139: S125–S153.

628 Endler, J.A. and Basolo, A.L. (1998). Sensory ecology, receiver biases and sexual selection.
629 *Trends in Ecology & Evolution*

630 Ferguson, J.W.H. (1994) The importance of low host densities for successful parasitism of
631 diderik cuckoos on red bishop birds. *South African Journal of Zoology*. 29: 70-73.

632 Forstmeier, W. & Schmelz, H. (2011) Cryptic multiple hypotheses testing in linear models:
633 Overestimated effect sizes and the winner’s curse. *Behavioural Ecology and*
634 *Sociobiology*, 65 (1) 47-55.

635 Friedl, T.W.P. (2004) Breeding behaviour of the Red Bishop (*Euplectes orix*): a synthesis and
636 new observations. *Vogelwarte* 42: 178-190.

637 Friedl, T.W.P. and Klump, G.M. (1999) Determinants of male mating success in the Red Bishop
638 (*Euplectes orix*) *Behavioural Ecology and Sociobiology* 46: 387-399

639 Hartig, F. (2022) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed)
640 Regression Models. R package version 0.4.6, [https://CRAN.R-project.org/](https://CRAN.R-project.org/package=DHARMA)
641 package=DHARMA.

642 Hunter, H.C. (1961) Parasitism of the Masked Weaver *Ploceus Velatus arundinaceus*. *Ostrich*
643 32: 55-63. Jensen, R.A.C and Jensen, M.K. (1969) On the breeding biology of southern
644 African cuckoos. *Ostrich* 40: 163-181.

645 Jensen, R.A.C., and Vernon, C.J. (1970) On the biology of the Didric Cuckoo in southern Africa.
646 *Ostrich*, 41: 237-246.

647 Kokko, H. Jennions, M.D. (2008) Parental investment, sexual selection and sex ratios. *Journal of*
648 *Evolutionary Biology* 21: 919-948.

649 Krüger, O., Davies, N.B., Sorenson, M.D. (2007) The evolution of sexual dimorphism inartistic
650 cuckoos: sexual selection or coevolution? *Proceedings of the Royal Society, B* 274: 1553-
651 1560.

652 Law, C.J. and Mehta, R.S. (2018) Carnivory maintains cranial dimorphism between males and
653 females: evidence for niche divergence in extant Musteloidea. *Evolution* 72: 1950-1961.

654 Lawes, M.J., and Kirkman, S. (1996) Egg recognition and interspecific brood parasitism rates in
655 red bishops (Aves: Ploceidae). *Animal Behaviour* 52: 553-563.

656 Lawes, M.J. Slotow, R. and Andersson, S. (2002) Male nest building but not display behaviour
657 directly influences mating success in the polygynous Red Bishop, *Euplectes orix*. *Ostrich*
658 73: 87-91.

659 Lindholm, A.K. (1997). Evolution of host defences against avian brood parasitism. Ph.D Thesis,
660 University of Cambridge.

661 Lyon, B., and Gilbert, G. (2013) Rarely parasitised and unparasitised species mob and alarm call
662 to cuckoos: implications for sparrow hawk mimicry by brood parasitic cuckoos. *Wilson*
663 *Journal of Ornithology* 125, 627-630.

664 Mank, J.E. (2008) Sex chromosomes and the evolution of sexual dimorphism: lessons from the
665 genome. *The American Naturalist*. 173: <https://doi.org/10.1086/595754>

666 Mank, J.E. (2023) Sex-specific morphs: the genetics and evolution of intra-sexual variation.
667 *Nature Reviews Genetics* 24, 44–52. <https://doi.org/10.1038/s41576-022-00524->

668 Martinez, J.G., Soler, J.J., Soler, M. & Burke, T. (1998) Spatial pattern of egg laying and
669 multiple parasitism in a brood parasite: a non-territorial system in the great spotted
670 cuckoo (*Clamator glandarius*). *Oecologia* 117, 286–294. (doi:10.1007/s004420050660)

671 Metz, M. Klump, G.M., & Friedl, T.WP. (2009) Male nest-building behaviour and mating
672 success in the red bishop (*Euplectes orix*) *Behaviour* 146: 771-794.

673 Mokos, J., Scheuring, I., Liker, A., Freckleton, R.P. and Székely, T. (2021) Degree of anisogamy
674 is unrelated to the intensity of sexual selection. *Scientific Reports* 11, 19424.
675 <https://doi.org/10.1038/s41598-021-98616-2>

676 Moskát, C. and Hauber, M.E. (2019) Sex-specific responses to simulated territorial intrusions in
677 the common cuckoo: a dual function of female acoustic signalling. *Behavioural Ecology*
678 *and Sociobiology* 73:60.

679 Noble, D.G. (1995) Coevolution and ecology of seven sympatric cuckoo species and their hosts
680 in Namibia. Ph.D Thesis, University of Cambridge.

681 Owens, I.P.F. and Hartley, I.R. (1998) Sexual dimorphism in birds: why are there so many
682 different forms of dimorphism? *Proceedings of the Royal Society B* 265, 397-407.

683 Parker, G. A., Baker, R.R. and Smith, V.G.F. (1972) The origin and evolution of gamete
684 dimorphism and the male-female phenomenon. *Journal of Theoretical Biology* 36: 529-
685 553.

686 Payne, R.B. (1967) Interspecific communication signals in parasitic birds. *The American*
687 *Naturalist* 101:921.

688 Payne, R.B. & Payne, K. (1967) Cuckoo hosts in southern Africa. *Ostrich* 38; 135-143.

689 Payne, R.B. (2005) *The Cuckoos*. Oxford: OUP Oxford.

690 R Core Team (2015). *R: a language and environment for statistical computing*. Vienna, Austria:
691 *R Foundation for Statistical Computing*. <http://www.R-project.org/>.

692 Reed, R.A. (1968) Studies of the diderik cuckoo *Chrysococcyx caprius* in the Transvaal. *Ibis*
693 110: 321-331.

694 Rowan, M.K. (1983) *The doves, parrots, lorries and cuckoos of southern Africa*. John Voelcker
695 Bird Book Fund, Cape Town.

696 Royle, N.J., Smiseth, P.T., Kölliker, M. (2012) *The evolution of parental care*. Oxford: OUP
697 Oxford.

698 Runemark, A., Eroukhanoff, F., Nava-Bolaños, A., Hermansen, J.S. and Maier, J. (2018)
699 Hybridization, sex-specific genomic architecture and local adaptation. *Philosophical*
700 *Transactions: Biological Sciences* 373: 1-10.

701 Ryan, M. (1990) Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in*
702 *Evolutionary Biology*, 7: 157-195.

703 Shine, R. (1989) Ecological causes for the evolution of sexual dimorphism: a review of the
704 evidence. *The Quarterly Review of Biology* 64: 419-461.

705 Székely, T., Reynolds, J.D. & Figuerola, J. (2000) Sexual size dimorphism in shorebirds, gulls,
706 and alcids: the influence of sexual and natural selection. *Evolution* 54: 1404-1413.

707 Therneau, T.M. (2015) *coxme: Mixed effects Cox models*. R package.
708 <https://cran.rproject.org/package=coxme>

- 709 Thorogood, R, & Davies, N.B. (2012) Cuckoos combat socially transmitted defences of reed
710 warbler hosts with a plumage polymorphism. *Science* 337, 578-580.
- 711 Thorogood, R. & Davies, N.B. (2016) Combining personal with social information facilitates
712 host defences and explains why cuckoos should be secretive. *Scientific Reports* 6, 19872.
- 713 Trivers, R.L., (1972) Parental investment and sexual selection. In: *Sexual Selection and the*
714 *Descent of Man 1871-1971* (B. Campbell, ed.) pp. 139-179. Aldine Press, Chicago.
- 715 Trnka, A., Prokop, P., and Grim, T. (2012) Uncovering dangerous cheats: how do avian hosts
716 recognise adult brood parasites? *PLoS One* 7:e37445.
- 717 York, J.E. and Davies, N.B. (2017) Female cuckoo calls misdirect host defences towards the
718 wrong enemy. *Nature Ecology and Evolution* 1: 1520-1525.
- 719 York, J.E., Wells, K.J. and Young, A.J. (2019) Dominance-related contributions to collective
720 territory defence are adjusted according to the scale of the threat. *Animal Behaviour* 158:
721 25-24
- 722 York, J.E. (2021) The evolution of predator resemblance in avian brood parasites. *Frontiers in*
723 *Ecology and Evolution* fevo.2021.725842.

724 **Author contributions**

725 J.E.Y. conceived the study, established the fieldwork project, carried out project administration,
726 secured funding, designed the experiment, collected and analysed the data, wrote the manuscript.
727

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743 **Open research**

744 Supporting data and code are provided and made available at datadryad.org and figshare.com on
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746

747 **Competing interests**

748 None.