

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:  $12.9 \pm 4.41$  seconds) than  
348 males ( $n = 23$ , mean  $\pm$  SE:  $49.4 \pm 16.3$  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 diederik 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 diederik  
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 diederik cuckoo compared to a female diederik 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 diederik 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 diederik 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 diederik cuckoo on the nest,  
401 hosts do not reject significantly more eggs after one day than when they observe a female  
402 diederik 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 diederik  
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 diederik cuckoo to lay undetected, those hosts that  
474 have observed a male diederik 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 diederik  
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 diederik'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 diederik 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, diederik  
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 diederik 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 diederik 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

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724 **Author contributions**

725 J.E.Y. conceived the study, established the fieldwork project, carried out project administration,  
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727

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742

743 **Open research**

744 Supporting data and code are provided and made available at [datadryad.org](https://datadryad.org) and [figshare.com](https://figshare.com) on  
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746

747 **Competing interests**

748 None.