

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

Jennifer York<sup>\*1,2,3</sup>

1. Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK.

2. Department of Zoology and Entomology, University of Pretoria, Hatfield, Pretoria, RSA.

3. Department of Ecology and Evolutionary Biology, Princeton University, 330A Guyot Hall,  
Princeton, USA.

<sup>\*</sup>jenny.e.york@gmail.com

## Abstract

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

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

## Introduction

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

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

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

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

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

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

## **Materials and Methods**

### *General methods*

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

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

### *Experimental design*

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

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

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

#### *Model bird stimuli*

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

#### *Behavioural responses*

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

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

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

### *Video analysis*

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

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

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

### *Statistical analyses*

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

### *Frontline aggression responses*

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

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

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

#### *Experimental brood parasitism egg rejection responses*

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

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

## Results

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

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

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

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

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

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

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

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

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

## Discussion

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

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

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

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

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

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

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

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

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

## Conclusions

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

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## **Author contributions**

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

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## **Open research**

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

## **Competing interests**

None.