Ritual displays by a parasitic cuckoo: nuptial gifts or territorial warnings?

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A R T I C L E   I N F O

In the sexual selection framework, nuptial gifts are materials a donor provides to a receiver that can increase the donor's fitness. In specific cases, sharing crucial information may be a nonmaterial nuptial gift. To investigate this hypothesis, we focused on the common cuckoo, *Cuculus canorus*, an obligate avian brood parasite whose reproduction costs of females are mainly related to finding host nests needed to lay their eggs. Nest searching is assumed to be conducted only by females. We hypothesized that males could contribute by transferring information on nest locations to females as a nonmaterial nuptial gift. Here, we show the results of a first step in this direction, in which we identified any behaviour potentially conveying information on nest abundance in the surrounding area, that is, behaviours whose frequency varied with host nest density. We conducted our investigation in a marshland area within the Po Plain (Italy), where we recorded both visual displays of cuckoos at perching sites, by using camera traps, and nest abundance of two of the most parasitized cuckoo host species, the reed warbler, *Acrocephalus scirpaceus*, and great reed warbler, *Acrocephalus arundinaceus*, by systematic nest monitoring. We found that male cuckoos adopted a certain posture, wing drooping, and tended to keep their tails up more frequently in areas with the highest versus lowest host nest densities. This is consistent with these behaviours acting as potential signals codifying information on nest abundance in the area. We finally discuss the implications of our findings for the mating choices of female cuckoos and the study directions warranted to reveal whether these displays and information transfer may be included as new elements of the sexual selection framework.

Darwin (1859, p. 88) first introduced the concept of sexual selection to account for phenomena not directly explainable by natural selection in a narrow sense. More than 100 years later, sexual selection is still one of the main research areas in biology and evolution, leading to an active debate on its definitions and observable effects (Alonzo & Servedio, 2019; Andersson, 1994; Clutton-Brock, 2017; Lindsay et al., 2019; Payne, 1984; Shuker & Kvarnemo, 2021). Brood parasites are one of the most challenging study models for sexual selection. Despite examples of brood parasitism found in insects and fishes, considerable scientific attention is focused on birds (Thorogood et al., 2019). By laying eggs in nests of other species, avian brood parasites do not suffer from a plethora of reproduction-related costs, such as those directly attributed to parental care (Feeney & Riehl, 2019; Kennerley et al., 2022; Krüger & Pauli, 2017). Accordingly, the criteria for female choice for a partner must rely on signals of male condition/genetic quality (i.e. indirect benefits, Andersson, 1994; Mitoyen et al., 2019) rather than male parenting skills. One such signal at the disposal of parasitic females might be nuptial gifts. According to Lewis et al. (2014, p. 2), nuptial gifts are 'materials (beyond the obligatory gametes) provided by a donor to a recipient during courtship or copulation in order to improve donor fitness'. Despite the definition focusing on the material nature of the items, evidence of birds providing inedible gifts (Pizzari, 2003; Stokes, 1971) suggests that under specific circumstances, the material composing the gift can be less relevant than the act of providing the gift itself.

Here, we investigated the potential presence of nonmaterial nuptial gifts in the common cuckoo, *Cuculus canorus*, a widespread

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avian brood parasite (hereafter, cuckoo). Cuckoos can parasitize over 100 host species, typically songbirds, with different populations targeting different hosts (Campobello & Sealy, 2009; Schulze-Hagen et al., 2009). During the reproductive period, cuckoo females are found, sometimes with overlapping ranges (Taborsky et al., 2004), in areas where their host species breed, whereas males seem to actively establish territories using vocalizations (Moskát et al., 2017; Moskát & Hauber, 2019; Xia et al., 2019). In avian brood parasites, fitness is strongly connected to their ability to deceive other species in raising their offspring, a process that starts with finding a large number of suitable nests, a task often attributed to females only (Feeney & Riehl, 2019; Honza et al., 2002; Krüger & Pauli, 2017). However, playback experiments showed that both male and female cuckoos pay attention to host alarm calls (Marton et al., 2019), supporting hypotheses on male–female cooperation in nest searching (Feeney & Riehl, 2019; Mikulica et al., 2017). Furthermore, anecdotal observations state that male cuckoos can distract host species, allowing females to lay their eggs, although video-recording studies failed to find evidence supporting this hypothesis in related parasitic species (Feeney & Riehl, 2019).

Accordingly, we hypothesized a role for male cuckoos in nest searching. They may facilitate females' nest finding by sharing information on host nest positions or abundance in the area. Doing so, they may improve female nest-finding success, or reduce the time females spend searching, thus resulting in a benefit for females. If females preferentially select males that provide this benefit, the transfer of information would increase the male's chances of being selected as a partner, increasing male fitness. This mechanism would fit the wider definition of nuptial gifts as information provided by a donor to a receiver that effectively increases the donor's fitness (Lewis et al., 2014).

The only available studies linking cuckoo behaviour to host nest attributes concern the rate of nest parasitism, thus focusing more on the host species than on the parasite itself (Clarke et al., 2001; Jelínek et al., 2014; Moskát & Honza, 2000; Stokke et al., 2007).

Esposito et al. (2021) provided the first insight into cuckoo behaviour at perches, finding that males are either vocal and motionless or silent and active. While several previous studies have investigated the role of cuckoo vocalizations (Davies et al., 1998; Moskát et al., 2017; Moskát & Hauber, 2019, 2021; Tryjanowski et al., 2018; Xia et al., 2019), the function of visual displays remains poorly explored. We verified whether the information on host nests is conveyed by specific postures or active motor displays acting as visual signals. Given its complexity, to assess whether a display may act as a nonmaterial gift, several aspects of cuckoo communication and patterns of evolution at the population level must be verified by multiple lines of research. Given the scant number of previous investigations, we addressed the first question along this path, whether visual signals convey information on host nests. If they do, we hypothesized that male cuckoos' ritual displays should be more concentrated in areas with a high host nest density. Accordingly, we first verified whether cuckoo abundance is related to host nest abundance, and second, whether the occurrence of specific behaviours depended on (1) the sex of the individual, (2) the presence of other cuckoos (i.e. an audience) and (3) the number of host nests in the area.

METHODS

We collected data in May–June 2022, in the 'Valli Mirandolesi' Special Protection Area (SPA–IT4040014). In particular, fieldwork focused on 16 partially flooded artificial basins in the wetlands surrounding Modena Ornithological Station ('SOM – il Pettazzurro', Mirandola, Italy; Fig. 1). This area has long been the study site for extensive research on individually and socially learned antiparasitism responses of cuckoo hosts (Campobello & Sealy, 2010, 2011, 2018). Reed warbler, *Acrocephalus scirpaceus*, and great reed warbler, *A. arundinaceus*, are among the most commonly parasitized species (Campobello & Sealy, 2009).
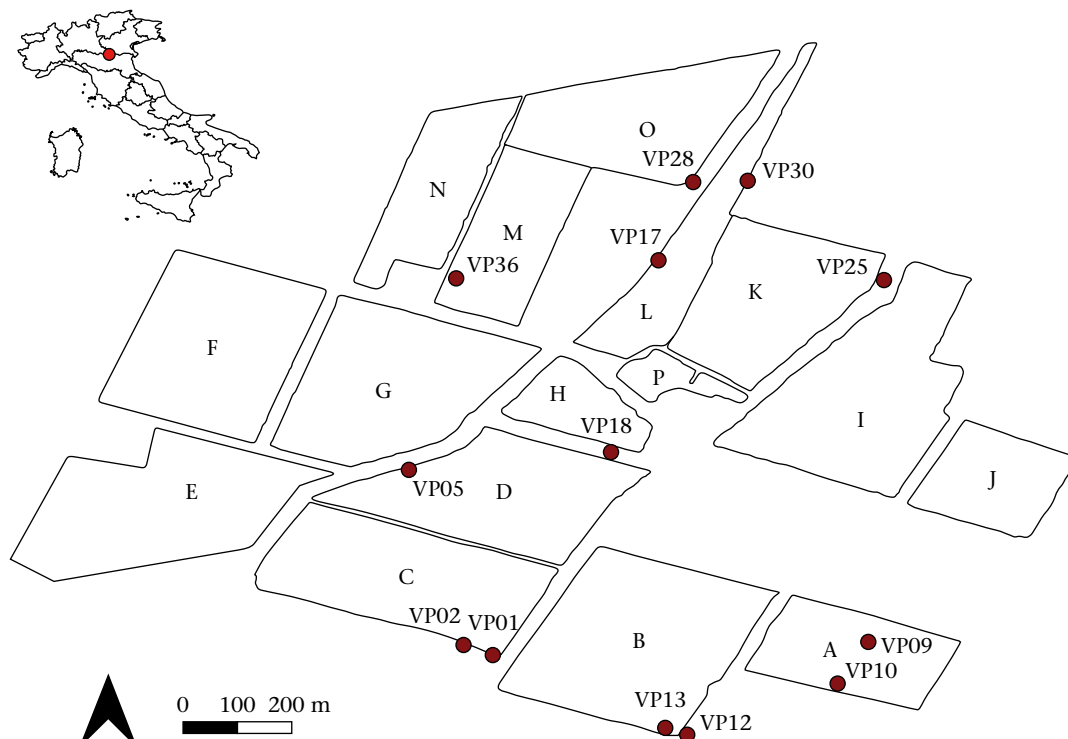

Figure 1. Study area map. Black polygons (A–P) are basins, while red points are the trees (vantage points, VP) where we recorded perched cuckoos' displays with camera traps.

Behavioural Observations

We conducted behavioural observations of perched cuckoos through videos realized by camera traps (Ziboni IDS Pro 4k 32MP) placed on 3 m metallic poles fixed on the ground at 3–10 m from selected vantage points (VPs, i.e. trees usually used by cuckoos to perch). We adjusted the camera trap orientation, exposure and field of view during the first few days of fieldwork and then we kept the settings consistent throughout the data collection. We set each camera trap to record 30 s videos (16 MP, 1920 × 1080) starting from any movement detected by the passive infrared sensor (PIR sensitivity: 'middle'; PIR interval: 5 s). We equipped camera traps with external SDs (SanDisk 128 GB) and rechargeable batteries (Melasta Ni−Zn, 1.6 V). We downloaded videos and charged batteries every 3–5 days. We monitored 13 VPs by 10 camera traps, from 23 May to 25 June 2022 (Table A1). We analysed videos with BORIS, an open-source event-logging software (Friard & Gamba, 2016), using a focal animal sampling approach (Altmann, 1974). We logged behavioural occurrences (binomial variables: 1 behaviour present; 0 behaviour absent) following the ethogram shown in Table 1. If the video showed the presence of two different cuckoos, we conducted two observation sessions, one per individual. We also recorded date, time, sex of the focal individual (M: male, if it performed the cu-coo call; U: undetermined, if it did not), number of individuals (number of cuckoos at the perch during the observation: 1: single; 2: dyad) and cuckoo orientation (the direction in which the cuckoo's head pointed for more than half of the video length, expressed through cardinal points: N, NE, E, SE, S, SW, W, NW).

Nest Searching and Densities

Six operators searched the reed beds across random transects and recorded the position of any reed warbler or great reed warbler nest, by using smartphone GPS receivers. To standardize nest searching, all operators searched all basins, thus keeping the sampling design as balanced as possible. Nest searching occurred from 10 May to 27 June 2022, at 0600–1000 and 1800–2100 hours (CET). We estimated basin nest densities by dividing the number of nests found in the basin by the product of the basin surface and the number of searching hours (no. of nests/km^2 × h). Basin surfaces were estimated by manually drawing polygons in QGIS 3.16.4, following basin borders on images from Google Satellite ('Quick-MapServices' plugin, see Tables A1 and A2).

Statistical Analyses

All statistical analyses were conducted in R (version 4.2.1) on RStudio 2022.07.1 (R Core Team, 2020). To explore potential links between cuckoo abundance at VPs and basin nest density we computed an estimate of cuckoo abundance per basin, as the number of cuckoo observations divided by the number of days of camera trap activity, aggregating data from different VPs associated with the same basin (see Tables A1 and A2). We used Kendall rank correlation (Kendall, 1975) to investigate the null hypothesis of no monotonic association between cuckoo abundance and nest density at the basin level (using the cor.test function), although the small sample size ($N = 9$) probably caused a low detecting power (Puth et al., 2015).

To determine whether sex, number of individuals and basin nest density were predictors of specific behaviours, we ran a series of generalized linear mixed models (GLMMs, maximum likelihood with Laplace approximation) with the function glmer ('lme4' package, Bates et al., 2015). Models were fitted on 388 of 397 cuckoo observations, to exclude missing values and obtain a more balanced data set (Mundry, 2014). In particular, we had no cuckoo observations from basins M and K, while we excluded basin O since we had only nine cuckoo observations and a low number of searching hours, leading to an uncertain nest density determination (see Table A2). The 388 observations refer to nine VPs (VP01, VP05, VP09, VP10, VP12, VP13, VP17, VP18, VP30), distributed over six basins (A, B, C, D, H, L). We used the occurrences of wing drooping, perched, tail up, tail swing and still as binomial response variables of five different GLMMs (logit link function), testing the effects of three predictors: sex (M or U), number of individuals (single or dyad) and nest density (covariate, range 0–32.46). We also included two random factors: orientation (eight levels) and time slot (131 levels). The latter is a unique identifier of every 2 h time slot at each VP across our study period, accounting for potential autocorrelation of subsequent observations at the same VP.

Table 1
Common cuckoo ethogram

Category	Behaviour	Description	Type
Postures	Wing drooping	Keeping wings lower than the tail. The wingtips point down	State
	Perched	Either moving or perching with wings above the tail, which is kept in a resting position	State
	Tail up	Keeping the tail up. The tail tip is higher than the head. Not swinging tail	State
Movements	Arriving	Entering the video frame and perching	Event
	Fly away	Exiting the video frame by flying away	Event
	Self-grooming	Preening own feathers	State
	Head movement	Moving head in any direction	State
	Tail swing UD	Moving tail up and down	State
	Tail swing LR	Moving tail left and right	State
	Moving	Moving on the branch or flying to another area of the perch, still in sight	State
	Still	Completely motionless	State
Vocalizations	Cu-coo	Two-note repeated syllables uttered by males	State
	Cu-cu-coo	Three-syllable call uttered by males	Event
	Gowk	Hoarse cough-like call	Event
	Gowk series	3–5 gowk-like calls uttered continuously	Event
	Guo	Similar to gowk, but lower and harsher	Event
	Bubbling	Long vocalization composed of a rapid sequence of high notes. Uttered by females	State
	Silent	Completely soundless	State
Interaction	Touch	Any conspecific interaction involving physical contact	State

Descriptions of postures and movements are adapted from Esposito et al. (2021). Vocalizations are defined according to Moskát and Hauber (2022) and Lei et al. (2005).

Time slot derives from the interaction of VP (nine levels), date (29 levels, from 23 May to 24 June) and time (nine levels, 2 h slots from 0500 to 2300). We excluded orientation from random factors in wing drooping, tail up and still models, to prevent singularities. The absence of collinearity among predictors was checked by examining the variance inflation factor (VIF, 'car' package, Fox & Weisberg, 2019), checking VIF < 2 for all predictors in all models (Mundry, 2014). We verified model assumptions by looking at a simulated residual qqplot and a simulated residual versus fitted values plot ('DHARMa' package, Hartig, 2022). To test model significance, we used a likelihood ratio test (LRT, Anova with argument test 'Chisq') comparing the full models (structured as stated above) to null models including only random factors (Dobson, 2002; Mundry, 2014). We also computed marginal and conditional R^2 values for full models (mR^2 and cR^2, respectively), following Nakagawa et al. (2017). We used the function r.squaredGLMM from package 'MuMIn' (Bartoń, 2023), reporting values associated with 'theoretical' method. Lastly, the function glmer shows P values based on the Wald Z test (Bates et al., 2015), but to obtain more conservative estimates of overall effects we again computed P values using LRTs, through the function drop1 (Luke, 2017). Several previous studies adopted similar statistical approaches (Gamba et al., 2016; Lacerte et al., 2021; Schlicht et al., 2023). We plotted results using packages 'ggeffects' (Lüdecke, 2018) and 'ggplot2' (Wickham, 2016).

Ethical Note

Our study design follows the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching and meets the Italian legal requirements (Permits number 24537/2022 from national ISPRA and number 10741/2022 from Emilia-Romagna Region). The use of camera traps greatly reduced the disturbance related to behavioural observations and we were extremely careful in nest searching, reducing to a minimum the time spent at the nest acquiring its position, to prevent any disturbance.

RESULTS

The camera traps recorded 22 376 videos, of which 5390 showed perched birds, including 397 with common cuckoos. We found 75 nests (eight great reed warblers and 67 reed warblers), of which 11 (14.6%, all reed warblers) were parasitized, distributed over 14 (of 16) basins (see Tables A1 and A2). Fig. 2 shows that cuckoos were not always concentrated in basins with higher nest densities (Kendall rank correlation: $\tau = -0.228$, $N = 9$, $P = 0.399$).

Table 2 shows the results of the full models. Among postures, wing drooping was more common in males and in areas with higher nest densities, while a perched posture showed the opposite tendencies, as expected. The probability of observing a perched posture was also higher for solitary individuals, whereas tail up, like wing drooping, was more frequent at higher nest densities (Fig. 3). Concerning movements, tail swing was more common in the presence of other individuals; however, the full model barely failed to explain the data better than the null one. Accordingly, being still was more frequent for solitary individuals and more common for birds of undetermined sex.

DISCUSSION

Our results showed that cuckoo males adopted a posture that was potentially able to convey information about a high host nest density: when perched within those areas, they drooped their wings and kept their tails up. In the presence of abundant host nests, they also tended to swing their tail when more than one individual perched on the same vantage point.
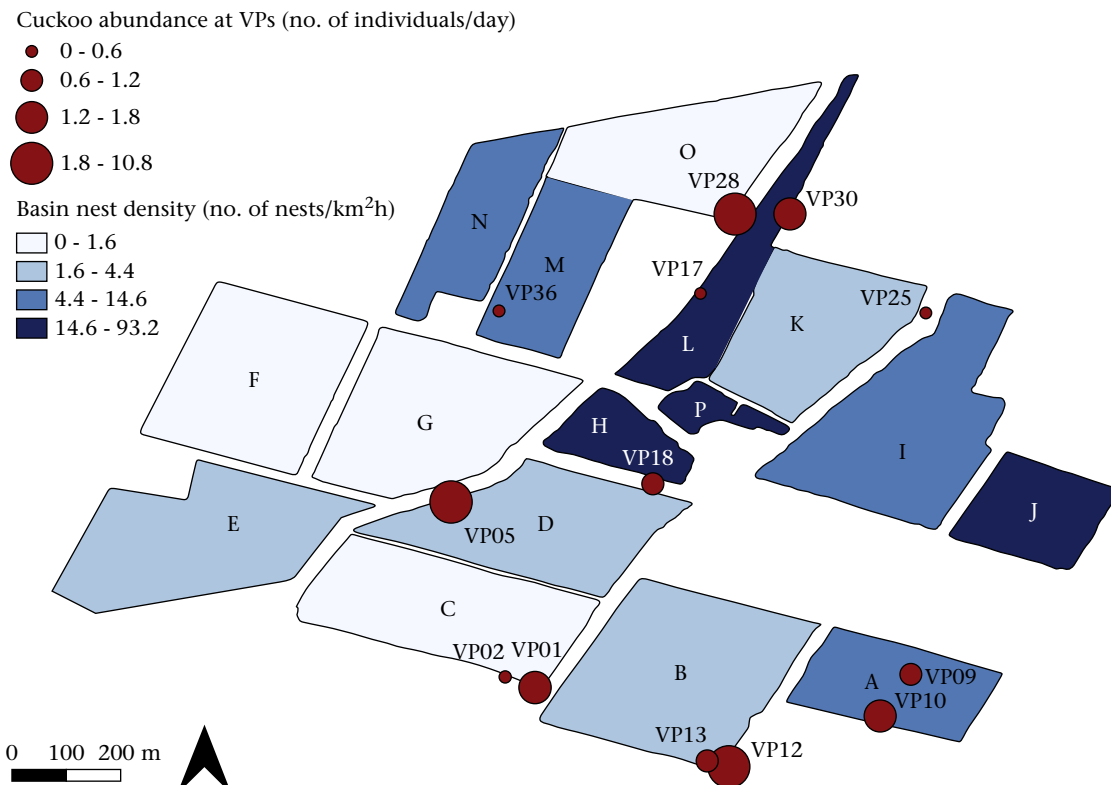
Figure 2. Cuckoo abundance at vantage points (VPs; dimensional scale, number of individuals/day) and basin nest density (blue scale, number of nests/km²h).

Table 2
Model results showing whether sex, number of individuals and nest density were significant predictors of specific behaviours performed by cuckoos at vantage points

	Estimate	SE	df	χ^2	P
Wing drooping					
Full model ($mr^2 = 0.10$; $cr^2 = 0.29$; full vs null: $\chi^2_3 = 17.992$, $P < 0.001$)					
(Intercept)	0.434	0.269			
Sex (male)	**0.795**	**0.308**	**1**	**6.433**	**0.011**
No. of individuals (dyad)	0.680	0.465	1	2.121	0.145
Nest density	**0.080**	**0.026**	**1**	**11.817**	**0.001**
Perched					
Full model ($mr^2 = 0.10$; $cr^2 = 0.27$; full vs null: $\chi^2_3 = 20.355$, $P < 0.001$)					
(Intercept)	0.123	0.283			
Sex (male)	**−0.780**	**0.293**	**1**	**7.025**	**0.008**
No. of individuals (dyad)	**−1.078**	**0.420**	**1**	**6.616**	**0.010**
Nest density	**−0.066**	**0.023**	**1**	**10.065**	**0.002**
Tail up					
Full model ($mr^2 = 0.06$; $cr^2 = 0.26$; full vs null: $\chi^2_3 = 9.332$, $P = 0.025$)					
(Intercept)	−2.213	0.385			
Sex (male)	0.509	0.371	1	1.924	0.165
No. of individuals (dyad)	0.676	0.452	1	2.104	0.147
Nest density	**0.062**	**0.025**	**1**	**6.585**	**0.010**
Tail swing					
Full model ($mr^2 = 0.04$; $cr^2 = 0.26$; full vs null: $\chi^2_3 = 7.586$, $P = 0.055$)					
(Intercept)	−2.277	0.361			
Sex (male)	−0.078	0.358	1	0.047	0.828
No. of individuals (dyad)	**0.938**	**0.438**	**1**	**4.330**	**0.037**
Nest density	0.047	0.025	1	3.675	0.055
Still					
Full model ($mr^2 = 0.18$; $cr^2 = 0.28$; full vs null: $\chi^2_3 = 23.662$, $P < 0.001$)					
(Intercept)	1.373	0.280			
Sex (male)	**−1.461**	**0.408**	**1**	**15.458**	**< 0.001**
No. of individuals (dyad)	**−1.227**	**0.430**	**1**	**7.246**	**0.007**
Nest density	0.032	0.030	1	1.227	0.268

Significant effects are in bold. Factors are dummy coded, 'number of individuals (single)' and 'sex (undetermined)' being the reference levels. mr^2 and cr^2 are marginal and conditional r^2 values, respectively.
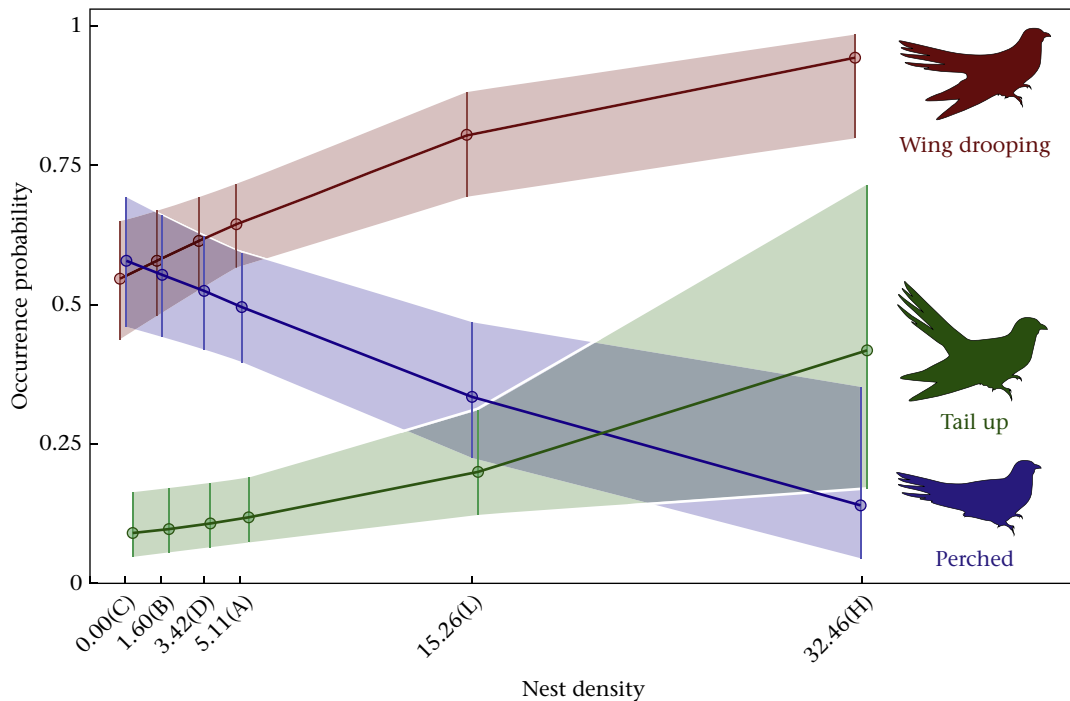
Figure 3. Occurrence of wing drooping, tail up and perched postures across increasing host nest densities. The x-axis shows nest densities in each basin (within parentheses). Plot shows marginal effects derived from full models (R function ggeffect). Marginal means are given ±95% confidence intervals.

Potential Visual Signals

Esposito et al. (2021) provided the first insight into common cuckoo motor displays, assessing that cuckoos are either vocal and motionless or silent and active, thus suggesting different communicative functions for the acoustic and visual components. The only studies focusing on cuckoo visual signals have investigated the role of female coloration (Krüger et al., 2007; Lee et al., 2019; York, 2021) or of chick begging displays (Grim, 2008; Rojas Ripari et al., 2021) in intra- and interspecific communication. Thus, this is the first work focusing specifically on displays of adult cuckoos potentially acting as visual signals. Specific postures or active motor displays are known to be effective as signals in the sexual selection dynamics of several bird species, including brood parasites (Barnard, 1990; Barske et al., 2011; Hamilton & Zuk, 1982; Rubenstein & Alcock, 2019). For example, O'Loghlen and Rothstein (2010) assessed the role of the wing-spread display of male brown-headed cowbirds, *Molothrus ater*, in eliciting a copulation solicitation response by females, when combined with vocalizations. Furthermore, the same display with a higher intensity is usually directed towards males, in situations that can escalate into physical fights, thus suggesting a role also in intramale competition (O'Loghlen & Rothstein, 2012). Similar behaviours involving certain wing positions may have a role in intra- and intersexual communication in other brood parasites, as well as common cuckoos.

Verifying the presence of a signal also entails investigating its origin, in terms of both behavioural evolution and communicative functions (Scott-Phillips, 2008; Smith & Harper, 1995). The peculiar wing drooping may derive from a posture effective in extending the body surface for thermoregulation or improving stability when perching, which could have been coopted in a signal conveying information, namely an exaptation (see Gould & Vrba, 1982). Brood parasitism in Cuculinae probably appeared around 10 million years ago (Krüger & Pauli, 2017; Sorenson & Payne, 2002), but because of the absence of information on the phylogenetic distribution of similar visual displays in sister taxa, we are not able to infer the posture's evolutionary history. We need further investigation to clarify whether wing drooping is a signal, that is, whether it influences the behaviour of other individuals. Results from our study are limited but consistent with a communicative function, although we could not disentangle whether wing drooping might have either intra- or intersexual communication roles.

Previous studies investigated the potential link between cuckoo behaviour and host nests but focused more on factors affecting the rate of nest parasitism (Clarke et al., 2001; Jelínek et al., 2014; Moskát & Honza, 2000; Stokke et al., 2007). One of the stronger predictors of parasitism is the nest distance from the closest VP (Clarke et al., 2001; Moskát & Honza, 2000). This evidence is consistent with both females using VPs to find suitable nests and males transferring nest information to females. Furthermore, Jelínek et al. (2014) suggested that cuckoos could adjust their nest-searching strategy depending on the number of available nests and, although we cannot exclude other factors, such plasticity could be the result of male−female cooperation mediated by male signals. A clue in this direction was provided by Marton et al. (2019), showing that both male and female cuckoos pay attention to host alarm calls, suggesting the presence of male−female cooperation in nest searching. Pair cooperation in nest finding has also been suggested for some socially monogamous avian brood parasites (Feeney & Riehl, 2019). In particular, according to opportunistic observations, males and females seems to search for host nests together in the black-headed duck, *Heteronetta atricapilla* (Lyon & Eadie, 2013) and in the screaming cowbird, *Molothrus rufoaxillaris* (Mason, 1987; Scardamaglia & Reboreda, 2014).

Nonmaterial Nuptial Gifts

We found specific cuckoo behaviours were more often performed in high nest density areas; thus, they could be potential signals conveying information on nest abundance to females or males. In the first case, the transfer of nest information might be a nuptial gift if donor males improve both their chances of mating and the female's fecundity. Indeed, a female that spends less time nest searching, after acquiring information from a male, may invest more energy in laying more eggs. An increase in male fitness related to enhanced female fecundity was reported by Lewis and South (2012) as one of the mechanisms by which a nuptial gift could increase donor fitness. Nuptial gifts usually come with a cost for the donor (Lewis & South, 2012), however, and, in this case, there are costs associated with nest searching and with performing a display, in addition to the time spent staying at the perch.

Under these circumstances, the information carried by potential signals could meet the requirements stated by Lewis et al.'s (2014) definition of nuptial gifts, that is, gifts that are (1) provided by a donor to a recipient during courtship or copulation and (2) effective at improving the donor's fitness. Despite the original definition focusing on the material nature of gifts, usually food items, examples of inedible gifts can be found in both arthropods (LeBas & Hockham, 2005; Martínez Villar et al., 2020, 2021) and birds (Pizzari, 2003; Stokes, 1971). In addition, the value of edible gifts in terms of energy intake is still debated (Morehouse et al., 2020, p. 42). Hence, it seems that the material composing the gift can be less relevant under specific circumstances than the act of providing the gift itself. On the other hand, the transfer of information is known to have a role in increasing fitness in other contexts (Galef & Laland, 2005), for example in patterns of social learning associated with bird information centres (Campobello & Hare, 2007; Ward & Zahavi, 1973) or foraging competence acquired by young through parental training (Galef & Laland, 2005; Lynch et al., 2020). The benefits of information transfer in the common cuckoo parasitic system have been extensively investigated, although limited to the host species. Specifically, hosts socially learn from conspecifics and heterospecifics to improve their efficiency in the frontline nest defence against parasitism (Campobello & Sealy, 2011; Thorogood & Davies, 2016; Tolman et al., 2021). Accordingly, signals providing information may also be associated with fitness benefits in cuckoos, playing similar roles to those of material items in the nuptial gift framework.

To our knowledge, there is no clear evidence of the presence of nonmaterial nuptial gifts, defined as such, in nature. Some findings, however, suggest similar mechanisms in other parasitic species. For example, male yellow-rumped honeyguides, *Indicator xanthonotus*, establish territories that include bee nests, giving access to females that select such males for reproduction (Cronin & Sherman, 1976; Payne, 1984, p. 27). Thus, male displays may indicate the presence of an accessible resource for females. Furthermore, Woolfenden et al. (2002), to explain their finding of a positive sexual selection gradient in brown-headed cowbird, *M. ater*, females, suggested that they may benefit from multiple mating by gaining access to host nests in several male territories. This stimulating hypothesis, however, still warrants specific investigation.

Alternative hypotheses might also explain our results. We can exclude that behaviour occurrence probabilities may be biased by having more cuckoo observations in some areas, because we did not find a correlation between cuckoo abundance and basin nest density. However, the correlation between a particular display and the basin nest density could derive from individual differences in behaviour associated with individual preferences for particular VPs/basins. Without the means to identify cuckoos individually, we cannot exclude such a scenario. However, the preference for a particular VP/basin could be associated with some forms of active

defence (i.e. territoriality) suggested by several previous studies (Moskát et al., 2017, 2019; Moskát & Hauber, 2019). In such cases, intramale territoriality would not be mutualistically exclusive with nonmaterial nuptial gifts. Indeed, if females select males by signals correlated with a proxy of male quality, and high-quality males establish territories richer in host nests, the link between displays and nest density would persist, making it possible to consider the signal itself as a nonmaterial gift. A similar situation occurs in the brown-headed cowbird, with females potentially selecting males by specific acoustic or visual displays (O'Loghlen & Rothstein, 2010, 2012) that may be correlated with male quality or physical condition (Cooper & Goller, 2004; Merrill et al., 2013; O'Loghlen & Rothstein, 1995). Unfortunately, evidence of high-quality males establishing territories in areas richer in host nests is still missing (Darley, 1982; Dufty, 1982; Yokel & Rothstein, 1991).

To properly verify the existence of nonmaterial gifts, we need to take at least two further steps. First, we need to assess whether the occurrence/frequency of male displays biases the female's mate choice. Second, we need to verify that female preferences for actively displaying males would eventually cause a net fitness benefit for some males, resulting in an observable sexual selection dynamic at the population level. In other words, we need evidence to broaden the definition of nuptial gifts into one that includes its possible nonmaterial nature, and thereby facilitates the receiver's access to a resource that cannot be directly provided by the donor itself, but not other signals or cues correlated with the donor's quality or general condition.

Conclusions and Perspectives

To conclude, we found two postures, wing drooping and tail up, more often performed in basins richer in host nests, potentially conveying information of higher parasitism opportunities. Since wing drooping is more common in males, this behaviour is a good candidate to be a signal to females, potentially acting as a nonmaterial nuptial gift. The tendency for males to preferentially perform tail swing in the presence of conspecifics needs to be verified with a larger sample size, but our findings suggest this behaviour has a role in some aspect of cuckoo communication. Further studies are needed to verify potential variations in displays under changing environmental conditions and during different stages of the breeding season. Also, combining camera trap observations with GPS-tagged individuals may help in revealing patterns of social association and territoriality, allowing us to verify whether they are consistent with our hypothesis. Further, using tagged individuals may enable us to identify potential individual variation in displays, and better assess the contribution of environmental factors in display occurrence, allowing us also to handle pseudoreplication issues. Lastly, a parentage analysis based on blood samples taken from chicks and focal adults would allow us to uncover an ongoing sexual selection process. While further investigations are required to assess the potential role of information acting as a nuptial gift, we obtained results consistent with our hypothesis. Working in this direction could help shed light on brood parasite communication and evolution processes, directly contributing to a better understanding of parasite–host interaction in hundreds of complex systems worldwide.

Author Contributions

Simone Ciaralli: Methodology, Formal analysis, Investigation, Data Curation, Writing–Original draft, Visualization. **Martina Esposito:** Investigation, Resources. **Stefano Francesconi:** Investigation. **Daniela Muzzicato:** Investigation. **Marco Gamba:** Formal analysis, Writing–Review & editing. **Matteo Dal Zotto:** Resources, Writing–Review & editing, Project administration. **Daniela Campobello:** Conceptualization, Methodology, Investigation, Resources, Writing–Review & editing, Supervision, Project administration, Funding acquisition.

Data Availability

The data set and the code are available as online supplementary materials.

Declaration of Interest

The authors declare no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available in the online version at https://doi.org/10.1016/j.anbehav.2023.11.003.

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Appendix

Table A1

Observations at vantage points (VPs)

VP	Basin	CT	Days of camera trap activity	Videos with perched birds	Other species	Cuckoo	Cuckoo abundance (no. of individuals/day)
VP01	C	CT06	14	1150	1129	21	1.50
VP02	C	CT07	4	58	58	0	0
VP05	D	CT08	14	550	399	151	10.78
VP09	A	CT02	23	577	552	25	1.09
VP10	A	CT03	31	993	943	50	1.61
VP12	B	CT05	14	377	333	44	3.14
VP13	B	CT09	25	184	154	30	1.20
VP17	L	CT10	24	757	742	15	0.62
VP18	H	CT11	12	80	65	15	1.25
VP25	K	CT07	4	45	45	0	0
VP28	O	CT07	3	59	50	9	3.00
VP30	L	CT04	20	552	515	37	1.85
VP36	M	CT07	5	8	8	0	0

Abundance was derived by dividing the number of cuckoo observations by the days of camera trap (CT) activity at the VP.

Table A2
Nest density and cuckoo abundance per basin

Basin	Area (km²)	No. of nests	Searching time (h)	Nest density (no. of nests/km²h)	Cuckoo abundance (no. of individuals/day)
A	0.070	9	25	5.11	1.39
B	0.151	7	29	1.60	1.90
C	0.122	0	9	0	1.17
D	0.112	5	13	3.42	10.78
E	0.135	2	7	2.12	
F	0.129	1	5	1.54	
G	0.132	2	12	1.26	
H	0.036	7	6	32.46	1.25
I	0.143	11	9	8.54	
J	0.057	16	15	18.60	
K	0.102	3	8	3.68	0
L	0.066	5	5	15.26	1.18
M	0.073	1	1	13.77	0
N	0.069	3	3	14.42	
O	0.101	0	2	0	3.00
P	0.016	3	2	93.15	

Abundance was derived by dividing the number of cuckoo observations by the days of camera trap activity at the vantage point, aggregating data per basin. This was not assessable in basins without sampled vantage points. Nest density was estimated by dividing the number of nests found in the basin by the product of the basin surface and the number of searching hours.