Multi-functional crest display in hoopoes *Upupa epops*

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Animals can engage in visual displays, which may target conspecifics, heterospecifics or both. Here we studied the function of the flamboyant crest-raising display of hoopoes *Upupa epops* in experiments performed with males in captivity. Males were exposed to sounds of a conspecific (male hoopoe song), a potential predator (human voice), and two controls (the song of a blackbird *Turdus merula*, and background noise). These stimuli were presented to males in the presence and absence of females. Males raised the crest with a significantly higher probability when confronted with stimuli indicating potential threats (rival mate or predator) than with controls. The crest display was frequent when confronted with both kinds of threats independently of the presence of a female, suggesting that it was directed to the predator and the rival male. The probability of raising the crest was not related to body condition, and there was a marginally but not significant negative relationship between probability of raising the crest and the number of black spots on the crest feathers, which may suggest that crest display could be informing about male quality. Therefore, male hoopoes display the crest in a heterospecific context in response to detection of potential threats, which could be a deceptive or pursuit-deterrent signal. The results also support a role of the crest in sexual selection, suggesting that crest display in male hoopoes may serve multiple functions.

Social interactions are a strong force driving the evolution of behaviour, morphology or physiology in animals (Westneat 2012), and they are, in most cases, mediated by communication (Ruxton and Schaefer 2011). Communication occurs when an individual (emitter) produces a signal (which can be of several different kinds, including visual, vocal and/or chemical), and the receiver makes decisions according to the information transmitted by the signal, with fitness consequences for the emitter (Endler 1993, Searcy and Nowicki 2005, Ruxton and Schaefer 2011).

In many cases animals elaborate behavioural displays amplifying the perception of morphology-based signals. For instance, visual signals are sometimes accompanied by a behavioural display (Bitton and Doucet 2014), so the signal becomes more conspicuous. Such displays are common in many taxa such as molluscs (Brown et al. 2012), arthropods (crustaceans, Arnott and Elwood 2010; insects, Brown and Porras 2015) and chordates (reptiles, Eifler and Eifler 2010; birds, Andersson and Iwasa 1996, Bitton and Doucet 2014; or mammals, Gol'din 2014). They may have evolved to amplify information conveyed in visual signals emitted to conspecifics (in intra- or intersexual contexts) as well as to heterospecifics. In the case of conspecifics, the displays of coloured morphological features may be involved for instance in sexual selection with individuals showing their ability to win contests (Steffen and Guyer 2014) or informing about their quality to potential mates (Memmott and Briffa 2015); also some traits may have both functions (Berglund et al. 1996).

In heterospecific contexts visual displays of coloured morphological features by prey may be directed to predators to inform about their unprofitability, thus increasing their probability of survival (pursuit-deterrent hypothesis, reviewed by Hasson 1991, Caro 1995). However, there are few known cases of animals in which the display of the same morphological features can serve as a multifunctional signal in different contexts (reviewed by Bitton and Doucet 2014). For example, tail-raising revealing bright red colour in the elegant trogon *Trogon elegans* is displayed both in the presence of conspecifics and heterospecifics (Bitton and Doucet 2014). That is also the case in the royal flycatcher *Onychorhynchus coronatus*, a passerine with an inconspicuous body except for a long crest of orange feathers with black tips which is usually hidden, but erected and exhibited in courtship and in antagonistic encounters with conspecifics and heterospecifics (Graves 1990, Rieveley 2010 cited in Bitton and Doucet 2014).

Crests are common ornaments among birds, and have been shown to convey information on individual quality and/or status both by their size (Jones and Hunter 1999, Daunt et al. 2003, Dakin 2011) and colour (McGraw et al. 2009, Remy et al. 2010), serving as intra- or intersexual signals to conspecifics. However, their potential to suddenly reveal conspicuous colour patterns when unfolded makes them suitable deimatic signals towards predators as those used by moths, mantis or amphibians (Umbers et al. 2015). Thus, they may inform potential predators of their detection

by the signalling bird, or its quality, as a pursuit-deterrent signal (Hasson 1991, Caro 1995).

In the breeding season (February to July), male hoopoes *Upupa epops* sing in conspicuous places to attract females (see more details in Martín-Vivaldi et al. 2004). They have a characteristic crest of orange feathers with a highly variable number of black tips (Martínez-García 2012) which is normally maintained folded, but can be fanned in a very conspicuous display (Fig. 1). This ornament is present and similarly coloured in both sexes, and is completely developed by nestlings at fledging. The display of crest feathers occurs in both sexes during the whole year and has been observed in social interactions with conspecifics (Simmons 1950), but also when birds are alarmed (Steyn 1967) or excited (Cramp 1998), and may therefore function in several different contexts. The black spots are very conspicuous not only when the crest is risen, but also when folded (Fig. 1), suggesting a prevalent signaling function. Black spots on feather tips have already been shown to constitute an important signal of quality in barn owls *Tyto alba* and kestrels *Falco tinnunculus* (Roulin et al. 2011, Piault et al. 2012), and therefore, they could inform about the competitive ability, partner value, or profitability as prey of a hoopoe to different receivers.

In the present study, we aim to analyse the function of the crest-raising display of the hoopoe. We experimentally studied the use of the crest display by male hoopoes exposed to playback of sounds simulating situations of an intraspecific conflict (the song of another hoopoe male), a potential predation risk (human voice), and two non-harmful control stimuli (blackbird song and background noise). If the crest display played a role in conspecific communication, we would expect that individuals displayed the crest when they listen another male singing. In addition, if the crest is also used in heterospecific communication, we would expect the crest to be displayed with a potential threat (Table 1). In this context, they would signal to predators that they were detected to provoke a change in predator behaviour, which could even give up hunting (pursuit-deterrent signal, Caro 1995). To test whether the presence of an audience affected the display behaviour of males, we performed experiments in which they were either in isolation or in the presence of females. This comparison will provide a test of whether the signal is directed to and affected by the presence of conspecifics in the two contexts (Table 1). We also measured male body condition and the number of black spots in the crest

Table 1. Framework of predictions for the different hypotheses (not mutually exclusive) of crest display function in hoopoes.

Hypothesis	Predictions for probability of crest display
Pursuit-deterrent signal	With predator > than with control stimuli
Warning alarm signal	With predator > than with control stimuli, AND more display in experiments with ♀♀
Intrasexual communication	Hoopoe song > control stimuli
Intersexual communication	Controls in experiments with ♀♀ > than in experiments with ♂♂ alone

of each individual. The number of black spots varies among individuals and is positively correlated with male reproductive success (Martín-Vivaldi 1997), and with testosterone titers in blood (Doña-Reguera 2013) in hoopoes. Therefore, in the case that the crest display reflects information about male quality, we would expect those variables being related positively to displaying behavior.

Methods

Study species

Hoopoes are medium size (25–29 cm) sexually dimorphic birds (Cramp 1998), recently proposed to be part of the Order Upupiformes (Mayr 2008) inhabiting Africa, Europe and Asia (Cramp 1998). Both sexes and juveniles have a highly conspicuous plumage with a black and white pattern in wing and tail feathers, and a crest.

Bird population

Between 2006 and 2014 we held in captivity a population of hoopoes in aviaries of the Univ. of Granada, each pair housed in independent cages of at least $3 \times 2 \times 2$ m. Individuals used for this experiment were born in captivity. Hoopoes had access to soil and they were provided with live food (crickets and fly larvae) and meat (beef heart) ad libitum every day. They reproduced normally inside the aviaries, where nest-boxes were installed.

Experimental procedures

Experiments were performed before breeding, from 13 February to 7 April 2009, only on sunny days to avoid changes in behaviour caused by rain, because part of the cages were uncovered. Tested males (n = 12, see below) were individually held in a large aviary ($4 \times 2 \times 2$ m) before trials for 24 h to habituate them to the experimental arena. Walls of the aviary were covered with a dense vegetation-like layer preventing birds from receiving external visual stimulus. Birds were supplied with fly larvae in a single feeder located on one side of the aviary that was replenished before each trial. On the floor, at about 1 m from the feeder, a loudspeaker (Elega CD-205, size 30×20 cm) was connected by cable to a computer that was outside the aviary, in order to start playbacks of experimental stimuli when birds went to feed. An observation cabin was located on the opposite side of the aviary from where the crest-raising behaviour of hoopoes in response to the stimuli was visually evaluated and registered. In addition,

Figure 1. A hoopoe male with the crest folded (left) and during the crest display (right).

two cameras were installed on both sides of the aviary (outside so hoopoes could not see them), and the entire event was video recorded for a more exhaustive subsequent analysis. All trials were carried out in the morning, starting at about 10:00 am. When the hoopoe approached the feeder and started to eat, the stimulus was played for 60 s.

Four different stimuli were presented to male hoopoes: as a conspecific sound, 1) a male hoopoe singing, since females do not sing. As a potential predator, 2) a person speaking. Despite the birds being born in captivity and their food was replenished every day, the contact with humans was very short (it took few minutes inside the cages), and we periodically caught them in the cages with mist nets. Therefore, hoopoes recognized humans as a threat and they were always frightened and ran or flew away when we entered the cages. In addition, since they were born in captivity, they never encountered a real predator, and they could not recognize sounds of natural predators that are not present at the Univ. (in the city). Thus, we used a stimulus that we were sure they would recognize as a threat. As a control stimulus, we used a heterospecific non-dangerous 3) blackbird song. There are numerous blackbirds around the cages during the entire year, and thus hoopoes were used to blackbirds. Finally, as a control to the experiment, we played 4) background noise in the loudspeaker. We observed that, when sounds started, hoopoes reacted quickly by raising their head (independently of display of the crest), but they never reacted to background noise, which indicates that they were not stimulated just by playing the loudspeaker.

All hoopoe sounds belonged to different individuals, and strophe length was similar (2–3 elements per strophe) to avoid different responses caused by the quality of males whose songs were used for playback (Martín-Vivaldi et al. 1998). Human voices were downloaded from different radio programmes, each from a different individual. Half of the sounds were from men and half from women to avoid bias due to different voice tones. Blackbird songs were also derived from different individuals, and the background noise stimulus was prepared by cutting and mixing silent parts of the other three sounds. Therefore, we never used one stimulus twice. In addition, each stimulus belonged to a different individual (human, blackbird or hoopoe), and the same

individual of each of those three species was never used twice. All four types of stimuli were played in the same conditions, with the same equipment, at the same volume (which was standardized for recordings before the experiments) (Fig. 2) and lasting 1 min exactly. The programme Adobe Audition was used to standardize the intensity of the stimuli. The order of presentation of the stimuli was randomly assigned in each experiment, and all combinations were used. After one sound was played we waited half an hour, and then the following was played when the individual approached the feeder and started to eat.

We performed two categories of experiments: a) with males alone, and b) including a female in a little cage ($1 \times 1 \times 1$ m) where the males could see her, placed beside the feeder. We used a different female for each trial, and the dyads were composed of individuals that did not know each other, i.e. they had not previously shared the same cage. We tested all males that were available because 1) they were in good condition, i.e. their behavior was apparently normal (flight and feeding), and 2) there was the possibility to make the second experiment with a non-relative female that they had not encountered before. Finally, there were a total of 12 individuals fulfilling these criteria, though one bird started breeding after the first experiment and was thus not tested in presence of females. All the experiments were included in the analysis. The trials including only males were conducted from 13 February to 14 March, while experiments with females were conducted from 16 March to 7 April. So, we finished all experiments of males alone before starting the experiments with females to allow males to rest between the two trials, in order to minimize effects of first playbacks. The breeding condition of the males was similar for all test subjects to minimize potential differences in motivation. Because we first conducted all the trials without a female and then all trials with a female, it could be argued that the males could have behaved differently during the second round of trials because of habituation to our stimuli. However, this possibility seems unlikely because birds were used to hear people and blackbirds every day, and also other hoopoe males since December–January, when they started singing in the cages. Therefore, no effects of an unknown stimulus in their response to sounds should be expected, or habituation in the
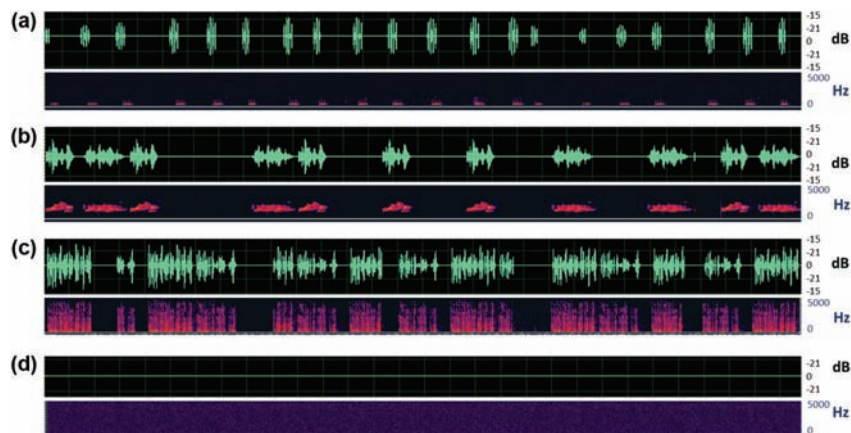

Figure 2. Envelop (decibels, up) and spectrogram (Hertz, down) of four different sounds: (a) hoopoe, (b) blackbird, (c) person and (d) background noise. This last one was made by cutting the silent parts of the other sounds.

second experiments (with females) due to first ones (males alone). The possible influence of difference in dates between experiments with and without females on our results is treated in the Discussion section.

Experiments and videos evaluation were performed by MRR. To assess the effect of knowing the stimuli, MMV and JMA watched 20 randomly selected videos separately and in blind condition, i.e. without sound, and they said if the crest was raised or not. The crest display is very evident (Fig. 1) and not possible to confound; actually, the coincidence among the 3 observers was of the 100%.

Measured variables

In each trial we recorded whether the male displayed its crest or not, and considered that the crest was displayed whenever it was completely open, which is unambiguous in this species (Fig. 1).

Visual displays may reflect the condition of the signalling individual. For example, potential partners might evaluate the health status of displayers (Loyau et al. 2005), or a potential predator could evaluate the profitability of hunting prey (Hasson 1991) through the emitted visual displays. For this reason, we also measured two quality-dependent variables in hoopoes and checked their relationship with the occurrence of crest displays during the experiments: body condition and the number of black spots on the crest feathers.

The total number of black spots in the crest was directly counted with the bird in the hand. Physical condition was calculated as the residuals of a linear regression of body mass on tarsus length ($R = 0.15$, $F_{1, 11} = 0.27$, $p < 0.001$). Residuals did not significantly correlate with wing length ($R = 0.32$, $F_{1, 10} = 1.19$, $p = 0.30$), indicating that our estimates are free of allometric effects (Green 2001). Since the two variables (number of spots and physical condition) were not significantly related to each other ($R = -0.41$, $p = 0.16$), both were included in the same model.

Statistical analyses

We used generalized linear mixed models (the Wald Chi square test) fit by the Laplace approximation with a binomial error distribution and a logit link function to assess differences in the probability of displaying the crest (yes or no) in relation to the category of experiment (males alones or males with females) and type of stimulus. Both variables were included as fixed terms and also their interaction, and

the number of black spots in the crest and body condition (both continuous) were included as covariates. Individual identity was included in the model as a random intercept because responses to different stimuli of the same individual are likely non-independent. Then, post-hoc comparisons were performed between each stimulus with the rest. We applied the false-discovery-rate (FDR) correction to establish the appropriate Q values in the post-hoc tests, which were the calculated p values after the FDR correction (Pike 2011).

Models were performed with the 'lmer' function implemented in the library 'lme4' of R environment (Bates et al. 2014). Degrees of freedom and p values were calculated through likelihood ratio tests.

Finally, we selected only the responses to control stimuli (n = 50 tests) and explored potential differences in male behaviour in the presence or absence of the female. The reason for this test is that with control sounds we would not expect responses caused by the stimuli, and we could detect differences in behaviour that could be attributed to the presence of females exclusively. This was calculated by means of a chi-square test in the Statistica 7.0 software.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.55062> (Ruiz-Rodríguez et al. 2017).

Results

The interaction between the type of stimulus and category of experiment was not significant (Table 2). The type of stimulus broadcast was related to the probability of displaying the crest by male hoopoes (Table 2). However, physical condition and the number of black spots did not reach statistical significance, although the latter presented a tendency to relate negatively to crest display (Table 2).

Males were significantly more prone to display their crests when exposed to the 'predator' sound (human) and with conspecific songs than they did with the two control stimuli (Fig. 3, Table 3). Human voice and conspecific song elicited the crest display with similar frequencies (Fig. 3, Table 3). All individuals opened their crest at least in one of the playbacks, and did not have significantly different proneness to display their crests (individual identity effect, $Z = 1.18$, $p = 0.24$).

Table 2. Results of generalized mixed models (Wald Chi square test) comparing the frequency of male responses, by raising the crest, when confronted with four different broadcasted recorded stimuli, and the influence of male quality estimates on their responses. Experimental category refers to experiments made to males maintained alone (♂), or in the presence of a female (♂ + ♀). Values in bold are statistically significant. BN: background noise.

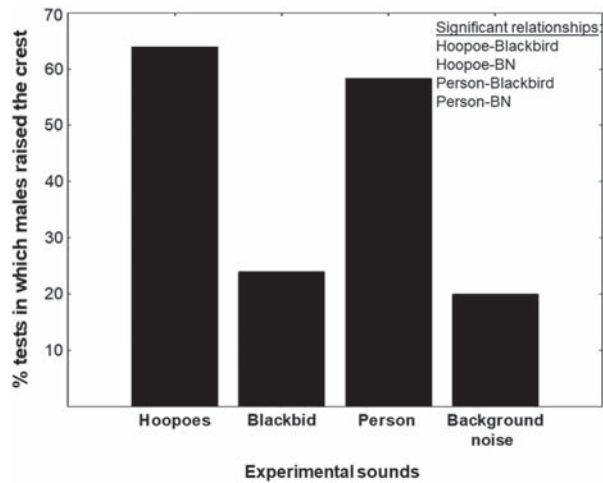| Predictor variable	X²	df	Estimate	SE	p
Stimulus	**20.62**	**3**	Hoopoe: 0.11	0.65	**0.0001**
			Person: −0.11	0.65	
			Blackbird: −2.07	0.70	
			BN: −2.37	0.73	
Experiment category	1.77	1	♂: −0.67	0.52	0.18
			♂ + ♀: 0.67	0.52	
Stimulus × Experiment category	4.89	3			0.18
No. black spots	2.75	1	−0.09	0.05	0.09
Physical condition	0.05	1	−0.06	0.08	0.47

Figure 3. Percentage of trials in which captive male hoopoes raised the crest in response to four different experimental stimuli broadcast.

The dispersion parameter was 1.10, which indicates that there is no overdispersion in the data.

When the control stimuli were played, males raised the crest more frequently in the presence of females than they did when they were alone ($\chi^2_1 = 4.72$, p = 0.03). This suggests that when a female is present, males raise the crest more frequently without threats or conspecifics stimuli, which may indicate that they do it to communicate with the female in the cage.

Discussion

Male hoopoes displayed the crest both when confronted with heterospecific (a potential predator) and conspecific stimuli (a potential male rival), suggesting that crest display in hoopoes serves multiple functions. The use of a signal in a context of predation risk may still be directed to conspecifics as an alarm warning (Hamilton 1964, Trivers 1971) apart from serving as a deimatic or pursuit-deterrent signal directed to predators. In that case there should be an effect of the presence of an audience on the use of the display (Murphy 2006). However, we have not found significant differences in the probability of raising the crest when hearing a potential predator in the presence or the absence of a conspecific. Although we are aware that the sample size was not very high, results are clear suggesting that male hoopoes

Table 3. Post-hoc comparisons of the frequency of male response by raising the crest among experimental and control stimuli, taking together experiments with only males and in the presence of females. Q corresponds to p values after the FDR correction. Values in bold are statistically significant. BN: background noise.

Comparisons	Z	p	Q
Person–blackbird	**2.80**	**0.005**	**0.007**
Person–BN	**3.06**	**0.002**	**0.006**
Hoopoe–blackbird	**2.96**	**0.003**	**0.006**
Hoopoe–BN	**3.22**	**0.001**	**0.006**
Hoopoe–person	–0.17	0.86	0.86
Blackbird–BN	–0.38	0.70	0.84

display the crest when they perceive the presence of a threat, independently of the presence of a conspecific.

The hoopoe is considered a highly unpalatable bird species (Götmark 1994), which could be due to volatile chemicals stored in the uropygial gland by females and nestlings during the breeding season (Martín-Vivaldi et al. 2010), as described for the closely related green woodhoopoe (Burger et al. 2004). In addition, experimental work has shown that hoopoes are actively avoided by raptors which may be able of discriminating their characteristics shape (Ruiz-Rodríguez et al. 2013). One of the most distinct attributes of hoopoe phenotype is its crest, even when it is folded (it extends several cm across the nape). Therefore, it is possible that the crest was the element reducing the probability of raptors attacking artificial hoopoe models (Ruiz-Rodríguez et al. 2013). This could well be the case because they recognize hoopoes by their shape and associate it with their unpalatability (Götmark 1994), but they could also recognize real hoopoes when they display the crest. In this sense, our results show that most hoopoes immediately raise the crest when they perceive a potential predator in the vicinity. Both the sudden flushing of the coloured crest and opening of the wings to fly with their contrasted black and white pattern may function as deimatic signals confusing or frightening predators (Umbers et al. 2015). Additionally, the crest could advertise potential predators of hoopoes' unprofitability as prey and thus functions as a pursuit-deterrent signal. In other bird species it was shown that a visual display is directed to predators, and thus it could potentially prevent predators from hunting them, such as in the elegant trogon (Bitton and Doucet 2014) and the turquoise browed motmot (Murphy 2006). More experiments testing the reactions of predators to the crest display of hoopoes are needed to assess its effectiveness in deterrence.

Isolated male hoopoes were more likely to raise the crest when they heard another male hoopoe than a control stimulus, suggesting that the display also functions in intrasexual competition with conspecifics. Hoopoe males use the song both to attract females before pairing (Martín-Vivaldi et al. 1999a, 2000) and to re-establish contact with their mate or respond to other males (Martín-Vivaldi et al. 1999a, 2004), but it has not been shown to serve as defence of feeding areas or territories (Martín-Vivaldi et al. 1999a). Our experimental males were unpaired, and, therefore, the main context in which the experimental song of a rival male could constitute a threat was in competition for females. Singing activity of hoopoes and therefore competition for potential mates starts in February–March, when the experiments took place. Indeed, in the recorded videos, we could see some males starting to sing in response to the playback, while others flew to a high perch and raised the crest. Given that the probability of use of the crest in response to experimental hoopoe song was high irrespective of the presence of a female, the most probable target of the crest display in this situation was the rival male.

Another result of our experiment is that males raise the crest more frequently with control sounds in the presence of the female, for which they could use the crest display in an intersexual context and directed to females. Other species such as the ruby-crowned kinglet *Regulus calendula*, which also possesses a coloured crest, displays it to potential

partners in sexual contexts (Martens and Päckert 2006). Although male hoopoes have been shown to signal their quality to females through strophe length of their song (Martín-Vivaldi et al. 2000), they may use both cues to show their condition. This is the case of the brown-headed cowbirds *Molothrus ater*, which during courtship perform a multi-modal display including songs and postural and wing movements (Hoepfner and Goller 2013).

Another possible explanation for changes in males' behaviour when they were alone or in the presence of a female, respect to control sounds, could be the effect of seasonality, since experiments with females were performed with about one month of delay. Reproduction in hoopoes takes place between February and July (Martín-Vivaldi et al. 1999b). Thus, although both were made at the beginning of the season, the motivation to find a female or the hormonal levels could have changed for the second assay. Our experimental design does not allow us to discard this possibility. In any case, the higher expression of this trait closer to reproduction would confirm a role during courtship either directed to females or to other males.

We have found that variation in the number of black spots in the crest was marginally but non-significantly related with variation in probability of crest display in the experiment. This implies that this display may potentially transmit information about male quality to both predators and conspecifics, including males and females. The sign of the effect on crest displaying is negative, which means that individuals with less spots open the crest more frequently. However, we would need a larger sample size to know if the effect is clear.

Black spots in the crest are positively related to hoopoe male reproductive success (Martín-Vivaldi 1997), body condition, and testosterone titters in blood (Doña-Reguera 2013), and negatively to body size (Doña-Reguera 2013). Therefore, potential partners may also cue in on black spots to estimate the quality of males. The non-significant, negative relationship between the number of spots and the use of the crest in intersexual contexts is difficult to interpret. It may depend on effects of testosterone on behaviour, less visibility of spots with the crest folded (Doña-Reguera 2013), or may indicate alternative strategies in courtship among males and will require new experiments to test the alternatives. Previous experiments with male fowls *Gallus gallus* showed that antipredator signalling was a good (positive) predictor of mating and reproductive success (Wilson et al. 2008). Therefore, male hoopoes with poorer condition could be trying to compensate this with their behaviour. Nevertheless, the results highlight the signalling function of the crest in this context.

Studying signals with multiple functions may help to understand evolution of animal communication in different ecological contexts such as predation or sexual selection. Displays in visual communication may amplify the emitted signal, and its use targeted to con- and hetero-specifics have been described in few cases until now (Bitton and Doucet 2014). The experiments performed with male hoopoes have shown that they display the crest to 1) heterospecifics: they target the display to potential predators, for which the crest could be functioning as a deceptive or pursuit-deterrent signal that advertises unprofitability; and 2) conspecifics: they display the crest when they heard another male singing,

regardless of the presence of females. Therefore, crest display in male hoopoes may be considered a multifunctional signal used in different contexts for communication with a variety of receivers.

The crest is a character present in both sexes of the hoopoe as well as in nestlings and fledglings, for which it may have a more important signalling function than that described here. For instance, both sexes could use crest features to evaluate other individuals, and it may play a role in parental–nestling communication. Future experiments should focus on the meaning of this signal in females and young hoopoes, but also in assessment of the crest display in relation to fitness.

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