

Are simple plumage traits sufficient for species discrimination by harrier males?

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I investigated whether plumage features are sufficient for species recognition in two sibling sympatric raptor species: the Montagu's harrier *Circus pygargus* and the hen harrier *C. cyaneus*. These species are similar in body size and differ slightly in plumage. During prelaying and laying periods, I placed artificial models close to nests of both species, simulating a conspecific male harrier (male of the same species), a heterospecific male harrier (male of the other species) or a wood pigeon *Columba palumbus* (acting as a control of the same size and colour). All of them represented birds perched in a neutral posture, so that they could only be recognised by their plumage differences. The use of plumage traits during this period would be particularly relevant in discriminating between their own and other species, offering the opportunity to avoid unnecessary fights, and therefore maximising the benefits of defence. I measured male responsiveness by recording aggressive behaviour towards each model (aggressive rate and time spent close to the female). Male presence time was significantly longer during conspecific decoy presentation than during heterospecific decoy presentation. Furthermore, males of both species were more aggressive towards the conspecific decoy than towards the heterospecific one, and no attacks towards the control were recorded. These results provide evidence that these birds are able to recognise plumage features of their own and the sibling species.

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Since Brown (1964) introduced the idea that the benefits obtained by territorial behaviour determine the level of investment in territory defence, numerous studies on aggressive interactions in birds during the breeding season have been made. In this period an individual could benefit by protecting nest sites and food (Orians and Willson 1964, Myberg and Thresher 1974, Cody 1978, Petrie 1984, Marden and Waage 1990, Stamps 1992), paternity, or offspring (Ewald et al. 1980, Gowaty et al. 1989, Birkhead and Møller 1992, Mougeot et al. 2001). Most descriptive studies focused on interactions between particular pairs try to describe the pattern of behaviour produced by each of these factors (Gowaty 1981, Wiklund and Village 1992, Karvonen et al. 2000, García and Arroyo 2002). Another set of studies consider questions such as how individuals respond to different type of intruders. For example, comparisons of territory owners' responses to intruding

neighbours versus their responses to intruding floaters (e.g. Temeles 1990), or aggressive rate towards conspecific intruders versus their responses towards heterospecific intruders (e.g. Elekonich 2000, García and Arroyo 2002). In contrast, underlying questions such as how birds can differentiate among different type of intruders have not been extensively studied and the literature is song-bird biased (Stoddard et al. 1990, Nelson 2000). Species recognition plays an important role in many aspects of avian ecology and behaviour, like mate choice, reproductive isolation or competition (Ptacek 2000, Irwin et al. 2001, Tang-Martínez 2001), and may also account for the differences of the intensity of aggressive responses towards different types of intruders.

Although birds may profit from aggressive behaviour during the breeding season, such behaviour also implies costs for individuals. First, the energetic costs of de-

fending the territory against intruders may reduce the fitness of residents (see Switzer et al. 2001). Second, in some species with powerful defensive weapons (claw, talons, beak), the injuries caused during fights are necessarily costly for individuals, and can negatively affect reproduction. In this context, discrimination among different types of intruders seem to be advantageous for individuals, because this enables unnecessary aggressive interactions to be reduced in order to minimise the costs of defence during breeding.

Several traits may be important for species recognition in birds, like differences in song (e.g. Lynch and Baker 1990, Slater and Catchpole 1990, Bretagnolle and Robisson 1991, Grant and Grant 1996), behavioural displays (see review in Ptacek 2000) and plumage patterns (Savalli 1995, Price 1998, Ptacek 2000). However, the relative importance of each of these traits may vary depending on the particular characteristics of the species, plumage being less important in species for which visual cues lose effectiveness, like in nocturnal birds (Bretagnolle and Robisson 1991, Bretagnolle 1996, Bretagnolle et al. 1998), or in birds with different plumage “phases”, in which mixed pairs are common (this includes raptors, melanistic birds, etc.; Newton 1979, Simmons 2000). In contrast, the importance of plumage features in discrimination should be crucial in species or in situations in which the risk of resource losses arises from individuals waiting in a neutral perching posture, when behavioural or acoustical cues are not enough to discriminate among intruders.

Despite the fact that in Montagu's harrier *Circus pygargus* and hen harrier *C. cyaneus* the function and context of aggressive behaviour have not been extensively studied (Bildstein and Collopy 1985, Maugeot et al. 2001, Garcia and Arroyo 2002), both species are known to engage in intraspecific and interspecific aggression and to often respond differently in the two situations (Garcia and Arroyo 2002). This suggests that harriers are able to discriminate among their own and other species (but see Murray 1971, for another explanation). However, to date, nothing is known about how individuals of these species recognize and discriminate among different intruders, and what traits are involved in such discrimination.

Previous studies on these sympatric harriers described the general pattern of aggression depending on the stage of breeding and the resource under competition (Garcia and Arroyo 2002). Overall, intraspecific aggression rate of both species peaked early in the season, and was mainly intrasexual and more frequent than interspecific aggression rate, supporting the idea that aggressive behaviour between males at this time was aimed at avoiding the costs of extra pair paternity. Since extra-pair copulations have been reported in both species (Picozzi 1984a, b for hen harrier, Maugeot et al. 2001 for Montagu's harrier), cuckoldry may represent a

high potential cost during reproduction. Furthermore, male harriers seeking extra-pair copulations might sit-and-wait for an opportunity in a neutral perched posture. At least in this context, the use of plumage traits would be particularly relevant in discriminating between their own and other species, offering the opportunity to avoid unnecessary fights, and therefore maximising the benefits of defence.

In this study I investigate whether simple plumage traits are sufficient for species recognition in sympatric harriers. The idea that fitness could be improved by reducing the costs of defence during the breeding season suggests that the capability of discrimination between intruders should be advantageous for males, which can estimate more correctly the trade-offs between costs and benefits of aggressive interactions at each moment. I set up an experimental design according to the following predictions: if male harriers can differentiate between conspecific and heterospecific intruders based just on plumage, both species should be more aggressive towards conspecific than towards heterospecific decoys (according to the patterns of aggressive behaviour described above; Garcia and Arroyo 2002). The other alternative is that male harriers cannot differentiate conspecific from heterospecific intruders based solely on plumage colour and pattern. If this is true, both species should show a similar aggressiveness towards conspecific and heterospecific decoys differing only in simple colour patterns. I tested these alternative hypotheses using models painted to mimic the plumage of each species. In addition, since model presentation did not involve variation in behaviour, body size, voice or complex plumage features (like feather brightness due to particular pigments, light refraction, etc., e.g. Hunt et al. 1998), this experiment provided a test of the efficacy of plumage traits in species recognition by harriers, which sheds light on the relationships between sympatric species.

Methods

Species studied

Montagu's and hen harriers are two ground-nesting diurnal raptors with similar body size (43 to 52 cm long, Del Hoyo et al. 1994). They differ in calls, display calls, and display structure (see Simmons 2000 for details) but, at least to the human eye, they only show slight differences in plumage. In both species, males have a grey appearance with pale underparts, black primaries and white rump. Hen harriers show a clear contrast between grey breast and white belly. Montagu's harriers have rufous-dotted underparts and a black strip on the upperwing, which hen harriers lack (Del Hoyo et al. 1994). Nevertheless, individual variation in the amount of grey and/or rufous on breast is high.

Females are hardly distinguishable by plumage alone, wing structure being the most reliable character to recognise them (hen harriers have broader and more rounded wings than Montagu's harriers; Del Hoyo et al. 1994, Forsman 1995).

Study area and experimental design

The study was conducted in May 1999 in Deux Sèvres (46°11'N, 0°28'W, Poitou-Charente region, western France), in an area of 340 km² devoted to intensive agriculture (for details see Arroyo et al. 1998). In total, 60 breeding territories of Montagu's harriers and 52 of hen harriers were found during the study year. I visited the nests three to five times during the breeding season to record clutch size. Laying and hatching dates were directly observed or derived from chick measurements (Arroyo 1995, own unpubl. data).

I used taxidermic mounts of harriers as a template to shape a polystyrene model with the same proportions as true birds (45 cm long) and a slimmer body intermediate between the two species. The use of models offers the opportunity to reduce differences between species just to plumage features, and it has been successfully applied in behavioural studies with harriers (Mougeot et al. 2001). I painted the model resembling adult males in a simplified way with respect to true birds: the hen harrier model was coloured slightly paler in the upperparts than the Montagu's harrier, and the Montagu's harrier model had a black band at the base of secondaries, and rufous-dotted underparts. Because the decoys represented perching individuals, underwing characters (rufous coverts and double black bands across secondaries in male of Montagu's harriers) were not represented. Both models had yellow iris and cere, typical of adult males of both species. As a control in the experiments, I used a plastic model of common woodpigeon *Columba palumbus* (manufactured by Sport Plast®, common in hunting activities) with similar size that harriers' models (45 cm long). To avoid unexpected responses due to 'weirdness' of the model I used a common woodpigeon as real as possible instead of the same polystyrene model used for harriers, although painted with grey coloration.

Experimental nests (30 Montagu's harriers and 23 hen harriers) were chosen based on visibility, accessibility and presence of recognisable individuals. Among Montagu's harriers, 13 males and 9 females carried wing tags, and other five males and seven females could be individually identified by plumage characters (double-banding on wings, dark plumage, moult extent, broken feathers, etc.). In hen harriers, four males and seven females could also be identified based on similar traits. Nevertheless, distance to the nearest neighbour was relatively large in this species (about 1000 m in average for the study population and year), so birds

moving around nests could be safely recognised as the territory owners.

All decoys were presented to each breeding pair in a neutral perching posture, without using any luring mechanism (such as playback or movement) that could confound the effect of plumage characters with other cues involved in species recognition. I examined the responses of males of the two species towards the models simulating conspecific and heterospecific intruders. All experiments were performed between the first week previous to laying and the end of laying, "pre-incubation" hereafter. Trials outside this period (sometimes determined from hatching dates as described above) were excluded from analyses. Models were presented at 1-day intervals, and the order of model presentation was randomized. I placed the models clearly visible in the surroundings of each nest, on a 65 cm tall stick situated 40 to 85 m away from the nest (exact distances were determined once the nest was located after experiments). The models were always placed when both the male and the female were out of sight (in hunting expeditions or at the nest). The location of models in relation to nests was the same in the three treatments (conspecific, heterospecific and control).

The behaviour of birds was recorded from a hide located 100-300 m away. Observations lasted 15 min counted since one member of the breeding pair arrived within 30 m from the model. I removed the decoy after 30 min if no individuals arrived. I considered that a male responded to the decoy when he approached to and flew around the model, regardless of whether he responded aggressively or not. Responses were measured as attack rate (in attacks min⁻¹, time registered from detection) and time spent by the male close to his female. Attacks included contacts with talons and aerial dives towards the model (Bildstein and Collopy 1985).

Because the experiments were carried out in different parts of the pre-incubation period of each pair, it is necessary to ensure that variability in the date of trials do not influenced results. For this, I used Spearman correlation to look for possible relationships between the aggressive response of each pair and the date of trial. By means of Spearman correlations I also checked for relationships between distance and observed responses. In other studies, attack rate increased with decreasing distance between decoy and nest-site (Mougeot et al. 2001). The distance between model and nest site was the same for the three treatments within pairs, but it varied slightly among pairs (40 to 85 m). It was necessary, however, to ensure that all pairs could be included in the same set of data (i.e. avoiding the use of pairs so far from the model that males did not perceived it as a threat).

Because all models were tested on the same individuals, I used a within-subject design to test for variation in attack rate towards conspecific and heterospecific models and also for the variation in male presence time

Table 1. Number of trial with attacks (and % of all observed individuals) against conspecific or heterospecific harrier models by Montagu's and hen harrier males, and attack rates (mean \pm SE) observed for each type of attack (aerial dives or physical contact).

	Trials with attacks (%)	Harrier model	
		Conspecific	Heterospecific
Montagu's harrier	6 (50%)		
Aerial dives (N = 6)		0.77 \pm 0.3	0.39 \pm 0.3
Physical contact (N = 1)		0.01	0.01
Hen harrier	12 (92%)		
Aerial dives (N = 12)		0.98 \pm 0.2	0.28 \pm 0.1
Physical contact (N = 9)		0.19 \pm 0.06	0.03 \pm 0.01

(that could indicate time employed by males in mate guarding). Harriers never attacked the control model, and hence this treatment was excluded from the analyses of attack rate. Non-parametric statistics (Wilcoxon matched pairs test) were used since attack rates significantly deviated from a normal distribution. A Wilcoxon matched pairs test was also calculated to check for statistical differences in the order of model presentation (effect of habituation), by comparing the responses to first decoy presentation with second decoy presentation, regardless of the type of decoy (conspecific or heterospecific).

Results

Territory owners were absent from the surroundings of the nest for longer than 30 min after placing the model in 17 trials, which were therefore excluded. Another 11 trials were excluded because males arrived less than 5 min before the end of the test (this served to avoid bias in attack rate due to the short time for observations). Twenty five males (12 Montagu's harriers and 13 hen harriers) responded to the presence of models. In all trials in which territory owners were present, males showed at least some interest in the intruder (for example, by getting close to it and flying around for a while), even when the control model was presented. However, harriers never attacked the control model, and hence it was excluded from the analyses of attack rate. In both species, males displayed two types of aggressive behaviour towards intruder models (Table 1). Aerial diving was the commonest aggressive behaviour exhibited by both species, observed in 12 trials for hen harriers and in six for Montagu's harriers. Physical contacts following aerial dives were observed in nine trials for hen harriers and in only one trial for Montagu's harriers. This type of behaviour was often intense in hen harriers, sometimes damaging the model's head. The frequency of trials with aggressive responses was significantly higher in hen harriers than in Montagu's harriers ($\chi^2 = 5.54$, d.f. = 1, $P = 0.018$; Table 1).

The observed aggressive rate was not significantly correlated with the date of the trial, either in hen

harriers (conspecific model: $r_s = -0.12$, $N = 13$, $P = 0.68$; heterospecific model: $r_s = 0.38$, $N = 13$, $P = 0.20$), or in Montagu's harriers (conspecific model: $r_s = 0.41$, $N = 12$, $P = 0.18$; heterospecific model: $r_s = 0.03$, $N = 12$, $P = 0.91$). The distance from the nest to the decoy was also not significantly correlated with aggression rate, either in hen harriers (conspecific model: $r_s = 0.12$, $N = 13$, $P = 0.68$; heterospecific model: $r_s = 0.23$, $N = 13$, $P = 0.44$), or in Montagu's harriers (conspecific model: $r_s = -0.30$, $N = 12$, $P = 0.34$; heterospecific model: $r_s = -0.29$, $N = 12$, $P = 0.35$).

Male presence time was significantly longer during conspecific decoy presentation than during heterospecific decoy presentation (Wilcoxon matched pairs test: hen harrier $Z = 2.66$, $N = 13$, $P = 0.007$; Montagu's harrier $Z = 2.52$, $N = 12$, $P = 0.011$). Males of both species attacked the conspecific model more often than the heterospecific model in all trials (Wilcoxon matched pairs test: hen harrier $Z = 3.06$, $N = 13$, $P = 0.002$; Montagu's harrier $Z = 2.20$, $N = 12$, $P = 0.027$; Fig. 1).

The order of the decoy presentation on a give pair did not affect aggressive response in both species. When responses to first decoy presentation was compared with responses to second decoy presentation, regardless of the type of decoy used, the test showed non-significant differences (Wilcoxon matched pairs test: hen harrier $Z = 0.63$, $N = 13$, $P = 0.53$; Montagu's harrier $Z = 0.94$, $N = 12$, $P = 0.35$).

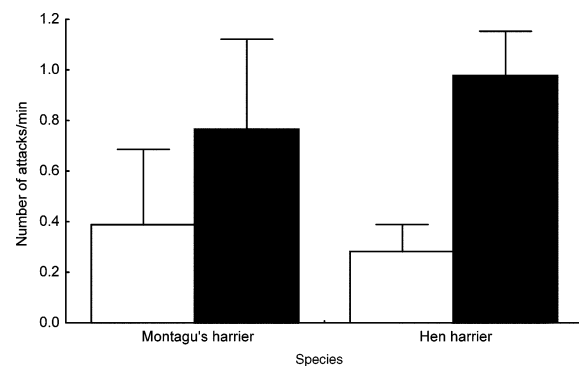


Fig. 1. Frequency of attacks (mean \pm SE) towards the conspecific (■) and the heterospecific (□) model by male Montagu's and hen harriers during the pre-incubation period.

Discussion

Already settled male hen and Montagu's harriers preferentially attacked models of their own species and guarded their females more often than in the presence of the other species. Experiments conducted during the pre-incubation period using models differing in colour pattern and excluding cues like behaviour or song, provided evidence that these birds are able to recognise plumage features of their own and the sibling species. This difference in response towards simulated conspecific and heterospecific intruders cannot be explained by individual variation in aggressive behaviour, because aggressiveness was measured on the same birds faced with each type of intruder. Nor could responses observed during the experiment be attributed to a lack of recognition of models as true birds, because both species ignored the control model (a wood pigeon, with the same size as potential intruders) and consistently showed a higher conspecific aggressive response than heterospecific aggressive response (as it happens in true social contests during the laying period, Garcia and Arroyo 2002).

The fact that both species attacked the heterospecific model, but that such aggression was less intense than intraspecific aggression, is consistent with aggressive responses observed in previous studies with real individuals (Garcia and Arroyo 2002). Within this period males respond to conspecific intruders as well as to heterospecific ones (which shared resources like food and nesting sites), but the latter were not competitors for mates and thus, the response was less severe.

In species in which males provide most of the food for females and chicks, such as harriers (Cramp and Simmons 1980), already mated males may prevent their mates from courting other males to avoid the costs of extrapair paternity (Birkhead and Møller 1992). During the fertile period of females, males perceived the presence of the conspecific model as an extra pair copulation risk (EPC risk), acting according to the risk perceived. The presence of the heterospecific models near the nest represent less of a threat for male owners, as paternity assurance was not at risk. Furthermore, males of both species increased their presence time close to the female in response to a male conspecific decoy as compared to a heterospecific decoy, even in the absence of physical aggression, suggesting that males guarded their mates in order to avoid EPCs. Such behaviour was observed in Montagu's harrier (Mougeot et al. 2001) in similar circumstances and the most likely explanation proposed by those authors is that female surveillance serves to protect females from extrapair copulation attempts by non-mated males, thereby also protecting paternity (Davis 2002). Although this result may be a by-product of male agonistic behaviour, since time present is needed to perform more attacks, this behaviour seems to be the most likely explanation for

the increase in male presence time after a simulated intrusion (Mougeot et al. 2001).

The prediction that males of both species can discriminate between their own and the other species on the basis of plumage features was confirmed by the intensity of male agonistic responses, both in aggressive rate and in time spent close to the females. Other cues like calls or courtship displays are also used in these species in many situations (see Simmons 2000). Nevertheless, courtship displays made by males (including calls and aerial displays) are more likely directed to territorial advertising or to female attraction. In contrast, discrimination among intruders by plumage features has its advantage in these species: EPC risk is highest just before and during the laying period (data for Montagu's harrier; Arroyo 1999), when females scarcely move from the nest (J. T. Garcia and B. E. Arroyo, unpubl. data) and the opportunity for males to get an extra-pair copulation depends on waiting –and perching– close to the nest. In this context plumage traits would be particularly relevant for recognition, as other behavioural cues lose effectiveness (they are not visible) when males stay perched.

Species recognition by plumage observed in harriers has important implications in ecology and biology, insofar as discrimination capability of males makes it possible for them to modulate their response against intruders according to the threat they represent, thereby reducing the overall costs of social contests (Temeles 1990). Aggressive behaviour in some species is generally unexpected because it conflicts with foraging. However, male harriers may trade foraging and mate guarding under certain circumstances, as suggested in other species (Birkhead and Lessells 1988, Simmons 1990, Korpimäki et al. 1996). In open landscapes, like agricultural habitats, female surveillance might be possible at long distances (Korpimäki et al. 1996, Mougeot et al. 2001), and male harriers may change their foraging behaviour, increasing presence time close to the female and forage around their nest (e.g. Mougeot et al. 2001). Through discrimination, males of these sympatric species may also try to avoid one another reducing the costs associated to aggressions towards heterospecific intruders previous to incubation, where the EPC risk is high.

In understanding how plumage may contribute to species recognition, it is important to know whether or not it is learned and from whom it is learned (Ptacek 2000). Recently, Shettleworth (2001) defined 'animal cognition' as the process by which animals take in information through the senses, process, retain and decide to act on it. In vertebrates, the mechanism underlying discrimination between own and others' phenotype seems to be recognition by association, which requires first learning the characteristics of a phenotype through previous association and then comparing this phenotype to the target's. The response behaviour is then dependent on perceived similarity

between the target and the own phenotype (see an overview in Tang-Martínez 2001). In harriers, like in other birds, individuals may learn conspecific traits as early as nestlings by association with their parents (Jouventin et al. 1999), or later on by experience with other conspecifics (Martens and Kessler 2000). According to my results, simple plumage traits like colour and plumage patterns would be incorporated to the learned 'template' to be compared with newly encountered individuals (Tang-Martínez 2001). This would allow harriers to modulate their response against intruders according to the threat they represent, thereby reducing the overall costs of social contests (Temeles 1990).

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