Adaptive significance of permanent female mimicry in a bird of prey

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Permanent female mimicry, in which adult males express a female phenotype, is known only from two bird species. A likely benefit of female mimicry is reduced intrasexual competition, allowing female-like males to access breeding resources while avoiding costly fights with typical territorial males. We tested this hypothesis in a population of marsh harriers *Circus aeruginosus* in which approximately 40 per cent of sexually mature males exhibit a permanent, i.e. lifelong, female plumage phenotype. Using simulated territorial intrusions, we measured aggressive responses of breeding males towards conspecific decoys of females, female-like males and typical males. We show that aggressive responses varied with both the type of decoys and the type of defending male. Typical males were aggressive towards typical male decoys more than they were towards female-like male decoys; female-like male decoys were attacked at a rate similar to that of female decoys. By contrast, female-like males tolerated male decoys (both typical and female-like) and directed their aggression towards female decoys. Thus, agonistic responses were intrasexual in typical males but intersexual in female-like males, indicating that the latter not only look like females but also behave like them when defending breeding resources. When intrasexual aggression is high, permanent female mimicry is arguably adaptive and could be seen as a permanent 'non-aggression pact' with other males.

Keywords: colour morph; alternative behavioural strategies; paternity assurance; marsh harrier; sexual dichromatism

1. INTRODUCTION

In the fierce competition for mating and survival, individuals that express alternative phenotypes rather than typical ones may gain fitness benefits. A good example is the expression, in males, of an alternative female phenotype to help reproduction

or to increase survival [1,2]. In the context of sexual selection, which typically favours conspicuousness in males (the selected sex) but dull coloration in females, males that are at a competitive disadvantage may gain fitness benefits from being less conspicuous, allowing them to access key breeding resources while avoiding costly interactions with other males. It is therefore not surprising to find sexual mimicry, whereby males express alternative female phenotypes, in many taxa, such as fishes, reptiles and insects [3].

Although female mimicry is also present in birds, it is usually restricted to earlier life stages: the plumage of young, sexually immature males is often female-like, but when males reach sexual maturity and reproduce they usually acquire typical male plumage. In some cases, males acquire the full mature phenotype with a time-delay after their first potential breeding season in a common pattern known as delayed plumage maturation [4]. In some other cases, however, female mimicry is expressed permanently. To date, this type of alternative phenotype has only been studied in a single bird species, the ruff *Philomachus pugnax* [5], a lek-breeding shorebird in which female-like males behave as sneakers to gain matings. Permanent female mimicry also exists in another bird, the marsh harrier *Circus aeruginosus* ([6]; electronic supplementary material). In central western France, this raptor species is characterized by a singular case of polymorphism in which a proportion of the breeding adult male population permanently (i.e. throughout their life) express a female plumage phenotype. This polymorphism is not owing to delayed plumage maturation but instead seems to be a consistent phenotype that is acquired in the second year and maintained as males become older. Although the adaptive significance of delayed plumage maturation and female mimicry in young breeding male birds is rather well studied [7], nothing is known about the adaptive significance of this singular case of polymorphism.

A main advantage of female mimicry is reduced aggression from other males [1]. Here, we tested whether male marsh harriers with permanent female-like plumage benefit from reduced aggression from other territorial males during breeding. The species is a polymorphic, socially monogamous, sexually dichromatic raptor: typical adult males have grey primary, secondary, greater coverts and tail feathers, whereas adult female plumage is mainly brown, with a white head and shoulder (figure 1). Female plumage overall lacks grey coloration, except in rare cases (less than 5%) in which old females display greyish coloration only on their primary coverts. In our study population, the breeding male population (i.e. adult males more than 2 years old) consists, however, of two contrasting plumage phenotypes: a typical male morph and a female-like male morph. Female-like male plumage is mainly brown and lacks grey on primary, secondary, coverts and tail feathers (unlike typical adult males). Female-like males differ from adult females in that they have slimmer and yellower tarsi and a pale iris (yellow-white in males, but ochre-brown in females; figure 1). Males are also approximately 30 per cent lighter and smaller than
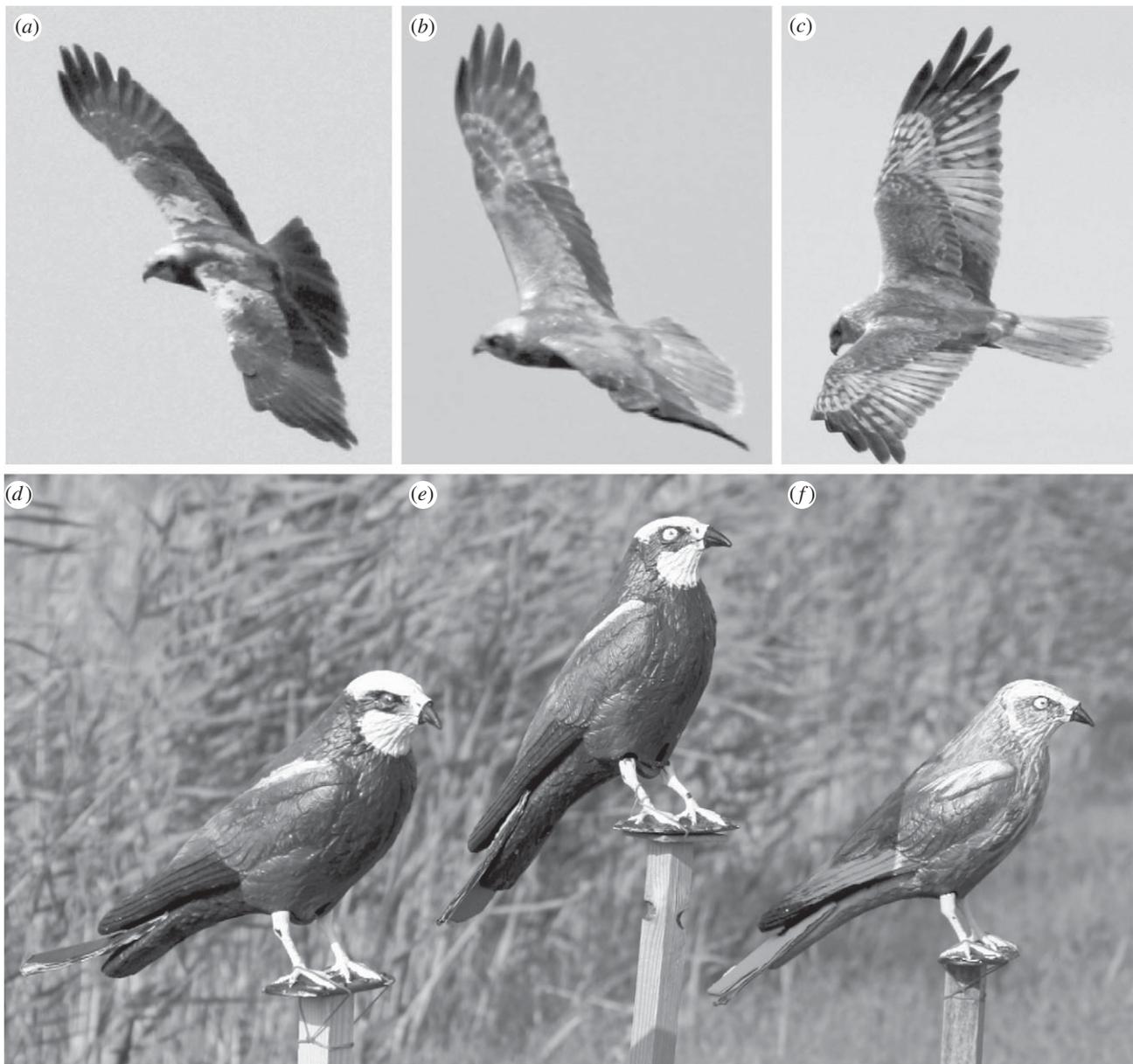
Figure 1. Adult marsh harrier plumage types from the study population: (*a*) female, (*b*) female-like male, (*c*) typical male, and decoy types used for experiments: (*d*) female, (*e*) female-like male, (*f*) typical male. (See electronic supplementary material for a colour version of the figure.)

females [6] (also see the electronic supplementary material for more detailed descriptions of plumage).

We used conspecific decoy presentations to experimentally simulate territorial intrusions near active nests. Territorial male raptors attack conspecific decoys, which are perceived as a threat to the territory/nest or to the male's paternity when the female is fertile, aggression being a common form of mate guarding [8]. We used three types of decoy, simulating intrusions by an adult female, an adult female-like male and a typical adult male. If a female-like male morph evolved to reduce intrasexual aggression, we predicted that males would be less aggressive towards female-like males than towards typical male intruders. In addition, because polymorphism in bird coloration is often associated with alternative behavioural strategies [9,10], we further investigated whether aggressive responses towards each type of intruder differed between typical and female-like males.

2. MATERIAL AND METHODS

(a) *Study area and pairs*
Experiments were conducted in March–July 2010 in central western France (*Marais de Brouage*; 45°51′ N–1°04′ W; electronic supplementary material). Nests were searched for in March–April and visited regularly to determine the breeding phenology of study pairs (see the electronic supplementary material). For each study pair, we classified breeding males as typical versus female-like, depending on the presence or absence of conspicuous primary and secondary grey feathers, respectively (from observation and digital photographs; electronic supplementary material).

(b) *Experiment*
We simulated conspecific territorial intrusions by presenting perched plastic decoys that had the shape of, and were painted like, marsh harriers (figure 1). Each study pair was tested with the three decoy types (female, female-like male and typical male; figure 1; electronic supplementary material) at three stages of the breeding cycle. Two replicates of each decoy type were used to ensure that the observed responses were not biased by some unique characteristic of a particular decoy (see the electronic supplementary material).

Each test was assigned *a posteriori* to one of three periods of the breeding cycle (relative to laying onset): fertile (prelaying and laying),

incubation, and chick-rearing periods (electronic supplementary material). Decoys were presented on a 1 m high perch near active nests. In each test, we quantified male attacks during 15 min starting after detection (i.e. when a harrier flew within 30 m of the decoy and reacted conspicuously to it). The decoy was not always detected by the focal male (nest owner) first, so we recorded who detected first (hereafter detector) and the amount of time during which the focal male was present and attacked the decoy, which averaged 13.7 ± 3.4 min. A similar procedure was used to record female aggressiveness towards decoys.

Tests were conducted on 36 pairs, with an initial aim of testing each pair with each of the three decoy types in each reproductive period. This was not always possible owing to fieldwork constraints or breeding failures. A total of 108 tests were conducted, with no pair being tested more than once with the same decoy type in a given period (see electronic supplementary material for sample sizes).

(c) Statistical analyses
We used SAS v. 9.2. The dependent variable (number of attacks) was fitted to generalized linear mixed models (Glimmix; SAS 2001) using a Poisson error distribution, with the duration of observations (time since detection by focal individual, log-transformed) included as an offset, to analyse variation in attack rates. Nest identity was included as a random effect. Initial models included the nest-decoy distance (covariate), detector (male or female of the tested pair, or another harrier), the reproductive period (fertile, incubation and chick rearing), the defending male type (typical versus female-like male), the decoy type (female, typical and female-like male) and their interaction as explanatory variables. We also included in this model the decoy replicate nested within the decoy type to test for possible differences in attack rate towards the two versions of a similar decoy type (electronic supplementary material). Non-significant ($p = 0.05$ level) terms were removed, starting with interactions, and following a backward stepwise procedure, until only the significant variables or interactions remained. Tests are two-tailed and data are expressed as means ± s.e.m.

3. RESULTS
Male aggressive responses only depended on the reproductive period ($F_{2,66} = 4.90$, $p = 0.010$), the decoy type ($F_{2,66} = 5.14$, $p = 0.008$) and the type of defending male in interaction with decoy type (defending male type: $F_{1,66} = 0.13$, $p = 0.716$; defending male type × decoy type: $F_{2,66} = 3.59$, $p = 0.033$; see also the electronic supplementary material). Overall, males attacked the typical male decoy (0.048 ± 0.025 attacks per minute, $n = 32$) more than the female-like male (0.028 ± 0.008, $n = 43$) or female decoy (0.033 ± 0.013, $n = 33$). Interestingly, aggressiveness towards different decoy types also depended on the type of defending male (decoy effect: typical males—$F_{2,33} = 11.81$, $p < 0.001$; female-like males—$F_{2,35} = 6.67$, $p = 0.003$; figure 2). When defending against intruders, typical males were aggressive towards typical male decoys significantly more than they were towards female decoys (Tukey–Kramer post hoc test; $T_{35} = -3.01$, adjusted $p = 0.013$) or female-like male decoys ($T_{35} = -2.78$, adjusted $p = 0.023$); female-like male decoys were attacked at a similar rate to that of female decoys ($T_{35} = 0.61$, adjusted $p = 0.814$). By contrast, female-like males never attacked the typical male decoys and were significantly more aggressive towards the female than the female-like male decoys ($T_{33} = -4.86$, adjusted $p < 0.001$).

Unlike males, females rarely attacked the decoys (0.015 ± 0.006 attacks per minute and 0.036 ± 0.009 for females and males, respectively). Overall, there was no significant heterogeneity in female attack rates towards the three decoy types (decoy type: $F_{2,74} = 0.92$; $p = 0.403$), although females tended to attack the female-like male decoys (0.023 ± 0.082 attacks
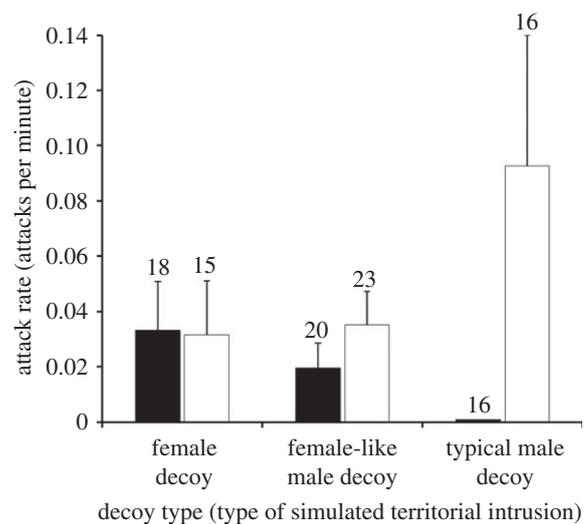
Figure 2. Aggressive responses (attacks per minute ± s.e.m.) towards the three decoy types (female, female-like male and typical male) depending on the type of defending male (white, responses of typical males; black, those of female-like males). Sample sizes equal number of tests.

per minute) more than the female (0.017 ± 0.053) or typical male decoys (0.010 ± 0.041).

4. DISCUSSION
As predicted, a female-like male intruder was less often attacked than a typical male, consistent with the idea that female mimicry reduces aggression from other males. Most interestingly, typical and female-like males differed in their aggressive responses towards the typical male intruder: the former strongly attacked it, whereas the latter never did. Female mimicry may therefore be adaptive, allowing female-like males to access key breeding resources (access to high-quality territories, extra-pair copulation opportunities) that could be too costly to obtain if they had to fight with other males. Specifically, reduced aggression may allow female-like males to establish territories (of potentially higher quality) near those of more aggressive territory-holders [11]. Consistent with this idea, in our study population, the average nearest neighbour distance between the nests of a typical male and of a female-like male (mean ± s.d.: 406 ± 316 m) was nearly half that between the nests of two typical males (727 ± 669 m; see the electronic supplementary material). In addition, the lack of aggression from female-like males towards typical male intruders might create a 'non-aggression zone' around typical males' breeding territories that could benefit the latter in several ways. First, direct aggressive interactions might be reduced through the presence of less aggressive (female-like) neighbours. Second, typical males might seek extra-pair copulations with the females of these less aggressive males [1]. Third, typical males might benefit from the greater involvement of female-like males in defence against predators, as it was experimentally shown that these are more aggressive towards predators on winter roosts [12].

In birds, individuals expressing different colour morphs behave in different ways [9]. In particular,

different melanin-based colorations (grey-black eumelanin-based versus rufus-brown pheomelanin-based plumages) are associated with different aggressive behaviours [10]. In marsh harriers, typical 'grey' and female-like 'brown' males may therefore differ in the relative concentrations of eumelanin and pheomelanin pigments in their feathers, resulting in different aggressive personalities [12]. Overall, we did not find that female-like males were less aggressive than typical males. Rather, we found different patterns of aggression in relation to specific intruder types: agonistic behaviour was directed towards typical males in typical males (i.e. intrasexual), but was more directed towards females (i.e. rather intersexual) in female-like males. Therefore, female-like males not only look like females, but also tended to behave like them [5] when defending breeding resources.

To our knowledge, the marsh harrier and the ruff are unique among birds for presenting a permanent female mimic morph in some adult males. We have shown that a main benefit of female-like plumage in males is reduced aggression from other males during breeding, as is usually found in young (sexually mature) males resembling females. More striking is that typical and female-like males appear to follow different aggressive behavioural strategies (intra-versus intersexual, respectively). To better understand the evolution and maintenance of such male polymorphism, more work is now needed to: (i) quantify genetic and environmental contributions to plumage coloration (and of female mimicry) in this species, and therefore, (ii) to assess whether the two types of males follow alternative reproductive strategies (mediated by genetic polymorphism) or conditional reproductive tactics (mediated by individual status) [3].

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