



Paternity assurance responses to first-year and adult male territorial intrusions in a courtship-feeding raptor

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Extrapair paternity occurs in many bird species and males use mate guarding, aggression or frequent copulations to reduce the risk of losing paternity. Because paternity assurance behaviour is likely to be costly, it should be adjusted to varying levels of perceived risk. We evaluated experimentally the adjustment of paternity assurance behaviour to risk in a raptor in which courtship feeding occurs: the Montagu's harrier, *Circus pygargus*. We used decoys with or without prey to simulate territorial intrusions by adult or first-year males. Inexperienced first-year males should represent a lesser risk than adult males and decoys with prey should represent a greater risk than those without prey, because courtship food could be traded for extrapair copulations. Aggression was less intense towards first-year than adult males during the female's fertile period. However, when decoys were presented with prey, aggression was similar towards first-years and adults. Males increased their short-term copulation rate in response to male decoys, particularly those presented with prey. Males also increased copulation duration, but only in response to adult male decoys. Our results show that male Montagu's harriers can fine-tune their paternity assurance behaviour to varying levels of risk, in this case the type of territorial intrusion. We also discuss the implications of our findings for the adaptive significance of delayed maturation in plumage colour in this species.

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Extrapair copulations (EPCs) occur in a wide range of bird species and may result in extrapair paternity (EPP; Birkhead & Møller 1992, 1998; Westneat & Stewart 2003). Where males provide parental care, cuckoldry decreases the fitness of the putative father, and selection is strongly expected to favour male behavioural mechanisms that reduce the incidence of EPCs and their likelihood of resulting in EPP (e.g. Birkhead & Møller 1992). Two main, alternative paternity assurance strategies are usually found in birds: mate guarding and frequent copulations. Mate guarding is probably the commonest strategy, consisting of close monitoring of the female when fertile to prevent EPCs (Birkhead 1981; Birkhead & Møller 1992; Komdeur et al. 1999). The alternative strategy consists of copulating frequently when the female is fertile, to reduce the likelihood of EPCs resulting in fertilization (Hunter et al.

1993). This is because of a fertilization advantage to the last male to copulate before the ova are fertilized and to the male that contributes the most sperm (Birkhead & Møller 1998).

A frequent-copulation paternity assurance strategy is particularly expected in birds that cannot guard their mates efficiently because of ecological constraints. This is the case, for instance, in raptors, a group of species in which males invest heavily in reproduction by providing most of the food for the female and nestlings (Newton 1979). Courtship feeding by the male during the prelaying and laying periods, when the female stays close to the nest, implies that males have to leave their mate unattended while hunting, and therefore cannot mate-guard efficiently. Accordingly, there is evidence of a frequent-copulation strategy in most raptor species studied so far (e.g. Mougeot 2004), but some degree of mate guarding and aggression towards male intruders have also been shown in some species (e.g. Simmons 1990; Mougeot et al. 2002).

Paternity assurance behaviour (mate guarding, aggression and repeated copulations) is likely to be costly, and its intensity should therefore be adjusted to the level of risk

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(Westneat 1994; Komdeur 2001). Variation in risk might depend on the context, such as breeding density or the frequency of territorial intrusions, on the quality of intruding males or on whether intruders have anything to trade for an EPC (e.g. Birkhead & Møller 1992, 1998). For example, in raptors, a higher breeding density is associated with a greater EPC risk and the intensity of paternity guards increases with breeding density (e.g. Simmons 1990; Arroyo 1999; Mougeot 2000, 2004). In addition, in some species, EPCs are traded for direct benefits, such as food. For instance, in the osprey, *Pandion haliaetus*, poorly fed females are less likely to copulate with their mates (Mougeot et al. 2002) but are more likely to beg EPCs from visiting males, and have been observed trading these for courtship feeding (e.g. Poole 1985). Thus, in courtship-feeding birds such as raptors, intruding males with food should be a higher risk than males without food. Intruding males are also likely to differ in the risk they represent according to their individual quality. Females may engage in EPC either as a means to have their eggs fertilized by a male of higher quality or as a strategy to assess potential mates and facilitate mate change (Birkhead & Møller 1998). In both cases, high-quality males should represent a higher risk when intruding than low-quality males. In raptors, young males are inexperienced and less successful breeders (Newton 1979) and are less good foragers than older males (Kitowski 2003), and therefore age qualifies as an indicator of phenotypic quality. Thus, intrusions by young males should be perceived by territorial males as a lower risk of EPC than intrusions by adult males.

We investigated adjustment of paternity assurance behaviour to varying levels of perceived EPC risk in male Montagu's harriers, *Circus pygargus*, a semicolonial raptor species with high male parental investment and delayed plumage maturation (adult and first-year males are phenotypically distinct). This species is socially monogamous, but EPCs have been observed relatively frequently in colonial situations (Pandolfi et al. 1998; Arroyo 1999). Previous work in raptors showed that perceived EPC risk can be experimentally increased by using decoy presentations to simulate male territorial intrusions (Mougeot 2000; Mougeot et al. 2001). Male Montagu's harriers respond to simulated adult male territorial intrusions during the female's fertile period by attacking decoys and by increasing their short-term copulation rate and the duration of these copulations (Mougeot et al. 2001). We tested here whether the intensity of male paternity assurance responses (aggression, short-term increase in copulation rate or duration) varied according to the type of territorial intrusion that a male experiences when his female is fertile. We used decoy presentations to simulate territorial intrusions by first-year and adult males, and presented the decoys with or without prey (a dead mouse) to mimic a male with or without a courtship feed that could be traded for an EPC. We predicted that mated adult males should adjust their responses according to the perceived risk mimicked by decoys, and thus respond less intensely to a first-year male than to an adult male decoy, and less intensely to a decoy presented without rather than with prey. We also discuss, in view of the results, the

adaptive significance of delayed plumage maturation in this species.

METHODS

Study Areas and Species

We conducted the experiment in 1997–1998 in three study areas in western France, where Montagu's harrier populations had been monitored for 4–10 years (Marais de Rochefort: 45°57'N, 0°55'W; south of Deux Sèvres: 46°11'N, 0°28'W; Baie de l'Aiguillon: 46°24'N, 1°24'W). In this species, males feed their mates in the prelaying and incubation periods and contribute 80% of the food for the nestlings from hatching to independence (Arroyo 1995; Arroyo et al. 2004). The species is socially monogamous, but with low mate fidelity: the divorce rate is 86% and 89% for males and females, respectively (V. Bretagnolle & A. Leroux, unpublished data). Montagu's harriers copulate at a relatively low rate compared with other raptors (Mougeot 2004), achieving 28–45 within-pair copulations for a clutch (Arroyo 1999). EPCs have been observed, accounting for 3.4–7.8% of all copulations, all of which occurred during the presumed fertile period (Pandolfi et al. 1998; Arroyo 1999). They are more frequent in colonial situations, involving up to 28% of females in the larger colonies (Arroyo 1999). Montagu's harriers do not defend feeding territories (Arroyo et al. 2004), but they defend an area in a 50–200-m radius around their nest that we define as the breeding territory. Females spend most of the time between pair formation and incubation within this breeding territory. Further details on the species can be found in Cramp & Simmons (1980) and Arroyo et al. (2004).

Experimental Procedure

We simulated territorial intrusions by presenting decoys of male Montagu's harriers. Each test consisted of 2 h of continuous focal sampling of behaviour: 1 h without a decoy (control period) followed by 1 h with a decoy present (experiment). Decoys were plastic decoys of a carrion crow, *Corvus corone*, which we modified (head, bill, tail) to resemble a perched Montagu's harrier (same size, shape and posture) and painted as either adult or first-year male (see below). Decoys were presented on a 1.5-m-high pole in a conspicuous open area near an occupied nest. The same set-up was used for all pairs and tests. Pairs were presented with one of four experimental situations: (1) a first-year male decoy without prey; (2) a first-year male decoy with prey; (3) an adult male decoy without prey; or (4) an adult male decoy with prey. In western France, Montagu's harriers feed mainly on small mammals, especially common voles, *Microtus arvalis* (Salamolard et al. 2000). We used a dead house mouse, *Mus musculus*, as prey, which was left conspicuously at the feet of the decoy. The mice were supplied to us for feeding captive-reared Montagu's harriers, as part of a conservation programme for the species.

Adult and first-year males (i.e. males fledged the previous summer) are clearly recognizable from plumage differences (Cramp & Simmons 1980). Adult males have ash-grey upperparts with black outer primaries, and white belly and flanks with rusty streaks; the head and breast are also ash-grey. In the spring of the second calendar year, males still hold most of their juvenile plumage (Arroyo & King 1996), which is characterized by brown upperparts, orange belly and flanks, and dark secondaries, although they may have replaced a variable number of body feathers (particularly on the head and neck), and occasionally also part of the tail (Arroyo & King 1996). We painted the decoy of the first-year male with juvenile plumage, but with some grey in the head, breast, wing coverts and central tail feathers (see Forsman 1999 for an illustration).

We conducted tests on breeding pairs that were selected from the 50–80 nests found each year based on the presence of recognizable individuals (identified either from plumage traits or from patagial wing tags) and for the visibility and accessibility of the nest area (see Mougeot et al. 2001 for further details). We held all the necessary licences for catching and wing tagging Montagu's harriers (licence granted to V. Bretagnolle by the Centre de Recherche sur la Biologie des Populations d'Oiseaux, France). We made wing tags (7×4 cm) from flexible PBC-coated nylon. Analyses showed no significant effect of wing tags on either survival, mating or breeding success of Montagu's harriers (A. Leroux & V. Bretagnolle, unpublished data).

We placed the decoy when the male was absent. We tried to set up the decoy as close as possible to the nest site, but no closer than 25 m to avoid disturbing the female at the nest. However, the distance between the decoy and the nest site varied between tests (25–100 m), because of habitat or other constraints limiting access to the field and nest site area from a nearby track or road. Observations were made from a hide or from a car. During the 1-h control periods, we recorded the occurrence and duration (s) of within-pair copulations. During the 1-h experimental periods, we recorded detection time by the male (time between the beginning of the test and detection), the number of male attacks (dives) towards the decoy, and the occurrence and duration of within-pair copulations. Detection by the male was defined as when a bird flew within a 50-m radius of the decoy, and approached it (either to inspect it, by close circling, or to attack it). We calculated an attack rate (attacks/h) towards the decoy, as the number of dives divided by the time after detection by the male. We calculated copulation rate in a similar way.

Monitoring of breeding pairs included regular nest visits during the breeding cycle, and allowed accurate determination of lay date (Mougeot et al. 2001; Arroyo et al. 2002). We assigned each test with an a posteriori day number, relative to laying onset (day 0). The fertile period, and especially its onset, is little known in raptors. In the American kestrel, *Falco sparverius*, viable sperm storage duration averages 8 days (Bird & Buckland 1976) and it is usually assumed that female raptors are fertile during the week preceding laying (Mougeot

2004). In Montagu's harriers, copulation rate and male paternity assurance responses to male decoys (aggression, mate guarding and copulations) are greatest during the week before laying until the day before the last egg is laid, when the risk of an EPC resulting in EPP is greatest (Arroyo 1999; Mougeot et al. 2001). For this study, we considered only tests conducted between day –6 and the day before the last egg was laid (clutch size range 3–6 with eggs laid every 2 days; Arroyo et al. 2004), that is, when females were most likely to be fertile. Sample size included a total of 75 tests conducted on 33 different pairs (11 in 1997 and 22 in 1998). Each pair was tested on average twice (range 1–4), but only once with the same type of experiment (first-year or adult male decoy, with or without prey). Two consecutive tests on the same pairs were at least 2 days apart (range 2–7).

Statistical Analyses

We used SAS (SAS 2001) and Generalized Linear Mixed Models for statistical analyses. We fitted models to the data using the following error distributions and link functions: attacks towards decoy: Poisson error distribution, with a log function (and log of the number of minutes after detection as an offset); copulation rate: binomial error distribution and logit function (only one or no copulation was observed in control or experimental periods so copulation rate was fitted to models as a binomial variable); copulation duration: normal error distribution and identity link function. We included year and nest as random effects in all models, to account for potential variation in behaviour between years and for repeated measures on the same pairs.

RESULTS

Attack Rate Towards Decoys

The mean distance between decoy and nest site did not differ between the four experimental situations (first-year versus adult male decoy, with or without prey; mixed model: $F_{3,39} = 0.09$, $P = 0.96$). The average time to detection \pm SD was 17.8 ± 9.9 min ($N = 75$) and did not vary significantly with distance between decoy and nest site or with experiment type (mixed model: distance: $F_{1,36} = 1.00$, $P = 0.32$; experiment type: $F_{3,36} = 1.20$, $P = 0.32$; distance*experiment type: $F_{3,36} = 1.12$, $P = 0.35$). In contrast, male attack rate towards the decoy varied significantly with both the distance between decoy and nest site and the type of experiment (Table 1). Overall, attack rate increased with decreasing distance between decoy and nest site, was higher for adult than for first-year male decoy presentations and was higher when the decoy was presented with rather than without prey (Fig. 1, Table 1). However, the increase in attack rate with decreasing distance between decoy and nest was not consistent across experiment types (significant age*prey*distance interaction; Table 1). During first-year male decoy presentations, male attack rate was significantly higher when the decoy

Table 1. Effects of distance between decoy and nest site and decoy type (first-year versus adult male, with prey versus without prey) on male attack rate

	Male attack rate*	
	$F_{1,64}$	P
Distance†	65.15	<0.001
Age‡	16.38	<0.001
Prey§	13.73	<0.001
Age*prey	6.81	<0.05
Age*distance	11.07	<0.01
Prey*distance	9.14	<0.01
Age*prey*distance	5.12	<0.05

*The dependent variable is the number of attacks, with the (log of) time after detection (min) as an offset. The model was fitted to data (counts of attacks) with a Poisson error distribution and a log-link function and included nest and year as random effects (Glimmix procedure, SAS 2001).

†Distance between decoy and nest site, log-transformed.

‡First-year versus adult male decoy.

§Decoy presented with versus without prey.

was presented with rather than without prey ($F_{1,29} = 10.94$, $P < 0.01$; Fig. 1); it increased with decreasing distance ($F_{1,29} = 9.64$, $P < 0.01$), but did so only when the decoy was presented with prey (significant distance*prey interaction: $F_{1,29} = 7.37$, $P < 0.05$; Fig. 1). During adult male decoy presentations, attack rate did not differ significantly when the decoy was presented with or without prey ($F_{1,36} = 0.65$, $P = 0.42$; Fig. 1), but increased with decreasing distance to nest site ($F_{1,36} = 97.55$, $P < 0.001$) during both types of experiment (decoy with or without prey; nonsignificant prey*distance interaction: $F_{1,36} = 0.16$, $P = 0.69$).

Copulation Rate

We first tested for overall differences in copulation rate between control periods (C) and experimental periods (E), that is decoy presentations (CE effect). Copulation rate was significantly higher during experimental periods ($\bar{X} \pm SD = 0.42 \pm 0.49$, $N = 75$) than during control periods (C: 0.21 ± 0.41 , $N = 75$; mixed model: $F_{1,148} = 10.27$, $P < 0.01$) and copulation rate during experimental periods did not vary significantly with distance between decoy and nest site (mixed model: $F_{1,63} = 1.17$, $P = 0.28$). Second, we tested whether differences in copulation rate between control and experimental periods varied between experiment types, that is, when a first-year or adult decoy was presented (testing for a CE*age interaction), when the decoy was presented with or without prey (testing for a CE*prey interaction), or according to both decoy age and prey presentation (testing for a CE*age*prey interaction). Differences in copulation rate between control and experimental periods did not vary significantly with decoy age (Table 2). However, copulation rate was significantly explained by the CE*prey interaction, indicating that the increase in copulation rate between control and experimental periods was significantly greater when male decoys were presented with rather than without prey (Fig. 2). The effect on copulation rate of adding prey was consistent across decoy age groups (nonsignificant CE*age*prey interaction). Differences in copulation rate between control and experimental periods were not significant for first-year male decoys without prey ($F_{1,28} = 0.00$, $P = 1.00$) and for adult male decoys without prey ($F_{1,38} = 0.47$, $P = 0.49$). There was a tendency for higher copulation rates during experimental periods when first-year male decoys were presented with prey ($F_{1,34} = 3.07$, $P = 0.08$) and a significant difference when adult male decoys were presented with prey ($F_{1,42} = 6.01$, $P = 0.019$).

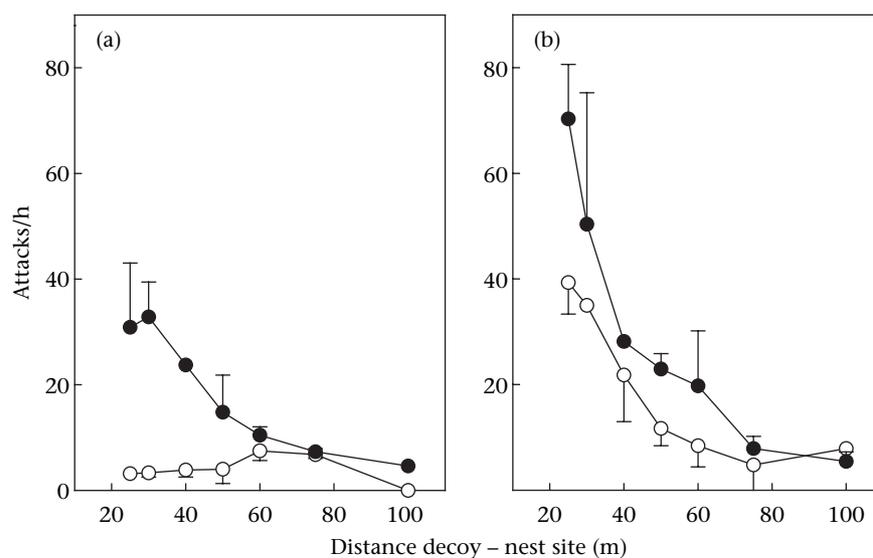


Figure 1. Male attack rate (dives/h; $\bar{X} \pm SE$) towards (a) first-year and (b) adult male decoys presented without (○) or with prey (●) and according to distance between decoy and nest site.

Table 2. Effects of decoy presentations (control versus experimental period, CE) and decoy type (first-year versus adult male, with prey versus without prey) on copulation rate and duration

	Copulation rate*		Copulation duration†	
	$F_{1,141}$	P	$F_{1,16}$	P
CE‡	8.23	<0.01	19.91	<0.01
Age§	0.45	0.50	2.47	0.14
Prey**	0.07	0.79	0.22	0.65
Age*prey	0.42	0.51	0.55	0.47
Age*CE	0.93	0.33	4.10	0.06
Prey*CE	4.32	<0.05	0.26	0.61
Age*prey*CE	0.03	0.86	0.14	0.72

*The model was fitted to data with a binomial error distribution and a logit-link function, and included nest and year as random effects (Glimmix procedure, SAS 2001).

†The model was fitted to data (within-pair copulation duration, s) with a normal error distribution and an identity link function, and included nest and year as random effects (mixed procedure, SAS 2001).

‡Control period (no decoy) versus experimental period (decoy presentation).

§First-year versus adult male decoy.

**Decoy presented with versus without prey.

Copulation Duration

Overall, within-pair copulations lasted longer when performed during experimental periods ($\bar{X} \pm SD = 5.4 \pm 0.9$ s, $N = 31$) than during control periods (4.2 ± 0.8 s, $N = 17$; Fig. 3, Table 2). Furthermore, the difference in copulation duration between control and experimental periods tended to be greater for presentations with adult male than first-year male decoys (CE*age interaction: $P = 0.06$; Fig. 3, Table 2). In contrast, copulation duration did not differ significantly between control and experimental periods when the decoy (regardless of age) was presented with or without prey (non-significant CE*prey and CE*age*prey interactions; Table 2).

DISCUSSION

Paternity Assurance Behaviour

Male Montagu's harriers have been observed breeding in their first-year, sometimes successfully, and are thus potentially sexually mature (Martelli 1987; Arroyo 1996). However, they do so extremely rarely, even though they often visit nest sites and colonies during the prelaying period, where they perform displays and food presentations, and where they attempt to copulate with females. This suggests that they are not very attractive to females. We thus predicted that they should represent a lower EPC risk than adult males. Our data supported this initial hypothesis. We found that male Montagu's harriers responded differently to first-year and adult male simulated territorial intrusions and, in particular, were less aggressive towards first-year males than to adult males. In response to adult male territorial intrusions, male attack rate towards the decoy increased rapidly with decreasing distance between the decoy and nest site, where the female spends most of her time before and during laying. Such a distance effect was not observed, however, for attack rate towards first-year male decoys presented without prey, which remained low even close to the nest area. A previous study showed very little aggression from males, and no distance effect, towards female decoys presented during the fertile period (Mougeot et al. 2001). Aggressive responses towards a first-year male decoy without prey were thus very similar to those observed towards a female decoy, although copulation responses were different (see below), as male Montagu's harriers do not increase short-term copulation rate in response to a female decoy presentation during the fertile period (Mougeot et al. 2001).

Although copulation rate did not vary significantly with decoy age, copulations performed during decoy presentations tended to last longer for adult decoys than for

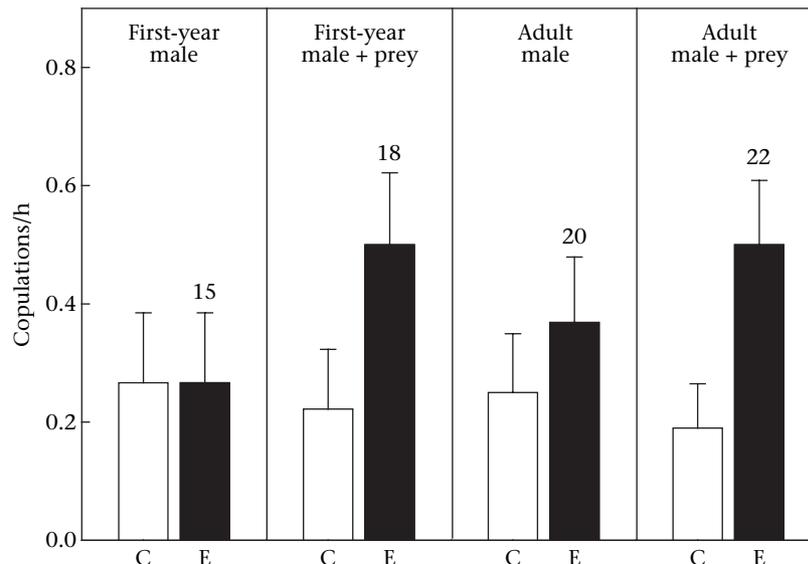


Figure 2. Mean \pm SE copulation rate (copulations/h) during decoy presentations (E; ■) and corresponding control periods (C; □) according to decoy type (first-year versus adult male, with prey versus without prey). Sample size, above bars, refers to number of tests.

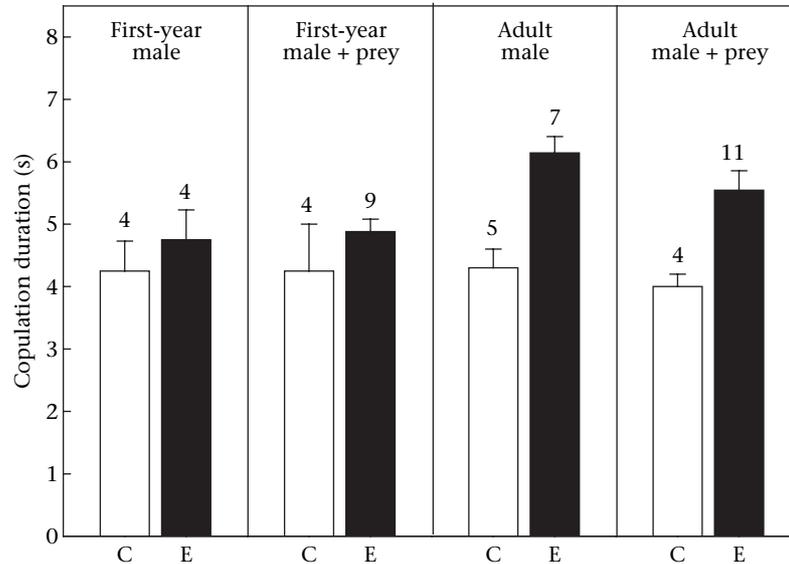


Figure 3. Mean \pm SE duration (s) of copulations during decoy presentations (E; ■) and corresponding control periods (C; □) according to decoy type (first-year versus adult male, with prey versus without prey). Sample size, above bars, refers to number of copulations.

first-year decoys, which is consistent with our initial hypothesis that male Montagu's harriers should perceive other adult males as a higher paternity risk than first-year males. Longer copulations are usually more likely to be behaviourally successful (i.e. to result in cloacal contact and sperm transfer; Mougeot et al. 2001) and could also result in increased sperm transfer. Both of these possible outcomes would be advantageous in terms of sperm competition (Birkhead & Møller 1998).

In addition, we predicted that a male intruder attending a nest area during the courtship period with prey should be perceived as a greater paternity risk, because females could trade EPCs for food (e.g. Poole 1985; Pandolfi et al. 1998; Mougeot 2000). In Montagu's harriers, copulation behaviour relates to courtship feeding, and 27–48% of copulations are preceded by a food pass (Pandolfi et al. 1998; Arroyo 1999). Within-pair copulation rate was positively correlated with courtship-feeding rate by the male during the early prelaying period but not later, suggesting that females may try to trade copulations for food during mate choice (Arroyo 1999). Copulations preceded by courtship feeding also last longer and are more likely to result in cloacal contact (Pandolfi et al. 1998). We found that copulation rate increased when the decoy was presented with prey (regardless of its age). We also found that adding prey to an adult male decoy had no significant effect on aggressive responses (although males tended to be more aggressive towards an adult male with prey than towards one without prey; Fig. 1), but adding prey to a first-year decoy greatly increased aggression. Aggression towards a first-year male decoy with prey also increased with decreasing distance between decoy and nest site, and was similar to that towards adult male decoys presented with or without prey.

The reason why first-year males almost never enter the breeding population is probably related to their lower foraging skills. They have a significantly lower hunting success than adults (Salamolard 1998; Kitowski 2003), and

are usually poor food providers (Martelli 1987). First-year males and females also often try to steal food from breeding birds (unpublished data). The only known case of successful breeding by a first-year male was of a male with a particularly high food-provisioning rate (Arroyo 1996). A first-year male that is able to present females with courtship food is probably of higher phenotypic quality, and might thus be perceived as a higher paternity risk than an average young male and elicit more intense aggression. First-year males thus seem to represent some degree of paternity risk, particularly when attending a nest site with courtship prey. Although most observed copulation attempts by first-year males are rejected by females (unpublished data), a successful EPC by a first-year male during the fertile period has nevertheless been observed (Arroyo 1999). In some cases first-year males have been observed acting as helpers, and delivering food to breeding females during the nestling period (Khan in Cramp & Simmons 1980; Cormier 1990). Females could thus also trade copulations with young males as a means to ensure some contribution later in the nestling period.

There is growing evidence that paternity assurance can be costly, in particular mate guarding and aggression, and that males adjust behaviour or resource allocation to their perceived risk of extrapair paternity (e.g. Møller 1987; Birkhead & Møller 1998; Komdeur 2001). Our experimental results, together with previous observations related to changes in copulation behaviour in varying breeding densities (Arroyo 1999), show that male Montagu's harriers can fine-tune their paternity assurance behaviour according to perceived risk.

Delayed Plumage Maturation

Our findings also have implications for our understanding of the adaptive significance of a gradual acquisition of adult plumage. Three main hypotheses have been

developed to explain why in some species (such as Montagu's harrier) young males have a different plumage to that of adult males, and resemble females (e.g. Conover et al. 2000). One hypothesis suggests that delayed sexual plumage maturation is a product of selection for delayed sexual maturation, so that males can benefit, in terms of survival (reduced predation or intraspecific aggression), from a cryptic plumage while unable to breed at a young age (Selander 1965). Although Montagu's harriers rarely breed at 1 year of age, this hypothesis seems unlikely given that predation probability is very low for a raptor such as the Montagu's harrier, and that intraspecific aggression is mostly restricted to short, specific times in the breeding cycle (such as the fertile period) in this non-territorial species (García & Arroyo 2002). The benefits of cryptic plumage for subadults are therefore probably not related to survival.

An alternative hypothesis, the 'female mimicry hypothesis' (Rohwer et al. 1980), states that young males avoid being attacked by older males by resembling females, and can gain territories or females through this deception. This hypothesis was supported for the European kestrel, *Falco tinnunculus* (Hakkarainen et al. 1993). However, unlike in the European kestrel, in which first-year male and female plumages can be similar, it is easy for an observer to tell a first-year male Montagu's harrier from a female, because the former have grey feathers. This suggests that first-year males are unlikely to be mistaken for females, as assumed by the female mimicry hypothesis. As mentioned above, females usually reject first-year males as mates or EPC partners, and nonbreeding birds are nonterritorial, so this hypothesis also seems unlikely to explain delayed plumage maturation in Montagu's harriers.

Finally, the 'status signalling hypothesis' states that first-year plumage, by honestly signalling subordination, allows males to avoid fights over resources in a dominance hierarchy (Rohwer et al. 1983; Rohwer & Butcher 1988; Grant 1990). Our results support this hypothesis. Aggressive behaviour of adult males at a critical stage of the breeding cycle was much reduced towards first-year males, which have a lower breeding status because of their inexperience and poorer foraging skills. Montagu's harriers are loosely colonial and, unlike other territorial raptors, show little intraspecific aggression, except when females are fertile; at this time, male-male aggression is strong and related to colony size (Arroyo et al. 2004). Reduced aggression towards individuals in nonadult male plumage at that time of the year may allow first-year males to visit colonies and prospect for future breeding sites without being perceived as much of a threat. However, our results also suggest that the perceived status of first-year males changed when they attended a nesting site with a prey item, when courtship behaviour, more than plumage, would indicate mating status or individual quality. Further work evaluating the reliability of such status signalling, and on the costs and benefits of subadult plumage, would nevertheless be needed to reach firmer conclusions.

In conclusion, we have shown that male Montagu's harriers adjust the intensity of their paternity assurance behaviour to varying levels of perceived risk. Decoy presentation experiments could similarly prove useful to

investigate adjustments of paternity assurance behaviour in other species.

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