ORIGINAL ARTICLE

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Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*)

Abstract We assessed whether colonial breeding allows individuals to decrease their investment in predator defence, by presenting decoys of owls, foxes and crows to Montagu's harrier, *Circus pygargus*. Decoy detection increased with colony size, as did the number of individuals mobbing the decoy. The number of mobbers was greater for predators potentially risky for the adults (owl or fox) than for non-dangerous predators (crow). Recruits (breeding neighbours, fledglings and non-breeders) were present a lower percentage of the time, and attacked and alarm called less frequently than tested individuals. Nevertheless, the overall attack rate on the predator increased with the number of mobbers. When the size of the mobbing group increased, individuals were more likely to attack predators that represented a risk for adults, but did so less intensively and with a lower frequency of close dives. Thus, coloniality decreased the individual costs of defence in terms of risk taken, whilst enhancing defence efficacy. Birds alarm called more intensively when presented with dangerous predators than with the crow. The number of recruits significantly increased with increasing alarm rate of the tested individuals, even when taking colony size into account. Furthermore, the alarm rate of the tested birds also had a significant effect on the proportion of recruits that engaged in attacks against dangerous predators but not against the crow. The higher recruitment and attack rates for dangerous predators were thus apparently modulated through alarm calling. We discuss whether tested birds may manipulate recruits' behaviour to lessen their own risk.

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Introduction

Group living is associated with costs, such as increased disease transmission, competition for food, breeding sites or mates, but also with potential benefits, such as transmission of information about food or mates and a decrease in predation risk (reviews in Bertram 1978; Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Brown and Brown 1996). For example, earlier predator detection and/or higher defence efficacy has been found in groups (Kruuk 1964; Hoogland and Sherman 1976; Robinson 1985; Møller 1987; Allainé 1991; Wiklund and Andersson 1994; Tella 1996).

An increased efficacy of active defence in groups may result from (a) the sum of each individual's investment or (b) an increase in the number of participating individuals compensating for a lower degree of individual investment (Allainé 1991), thus reducing individual costs. Costs associated with defence include the time spent in vigilance and defence to the detriment of other activities, the metabolic costs of attacks or alarm signals, as well as the risk of injury or death from the predator during attacks. Whether individual costs of defence vary according to group size is an important issue, because optimal group size ultimately depends on the per capita cost/benefit relationship (see Pulliam and Caraco 1984; Lott 1991; but also Giraldeau and Gillis 1985; Giraldeau 1988).

The influence of sociality on costs of defence has often been evaluated by relating time spent in vigilance with group size, especially in foraging vertebrates (e.g. Roberts 1996; Lima et al. 1999). Conversely, very few studies have evaluated individual investment in mobbing groups, for example in terms of attacks towards predators. Mobbing behaviour has potential direct benefits to the mobber in terms of discouraging or driving

away the enemy (Curio 1978; Curio et al. 1978; Elliot 1985b; Flasskamp 1994), but it also entails the greatest potential cost: a risk of injury or death as mobbers approach the predator (Curio and Regelmann 1986; Montgomerie and Weatherhead 1988). Therefore, whilst relying on a large group to deter a predator, individual investment should decrease to diminish the risk taken. This has been tested at an interspecific level (risk taken was greater in solitary- than in group-mobbing swallows; Brown and Hoogland 1986), but not at the intraspecific level, for example in considering how individual behaviour is affected when the size of the mobbing group varies.

Mobbing behaviour is usually mediated through the use of alarm calls (Bradbury and Vehrencamp 1998). Mobbing calls are alarm signals designed to maximise transmission to the predator and to conspecifics, to facilitate group formation and cohesion and/or manipulate the actions of conspecifics (Charnov and Krebs 1975). Communal defence may provide equal benefits to all group members but may, alternatively, be more profitable to the emitters of alarm calls than to reactors. Therefore, an asymmetry in the distribution of benefits gained might indicate that alarm signals involve deceit and exploitation of conspecifics.

We studied nest defence behaviour of Montagu's harrier, *Circus pygargus*, a medium-sized raptor that nests on the ground (rendering it potentially vulnerable to predation) either solitarily or in loose assemblages of up to 30 pairs (Krogulec and Leroux 1994; Arroyo 1995). These nesting strategies are combined with active anti-predator defence, the use of alarm calls and collective attacks (Cramp and Simmons 1980; Arroyo 1995). We assessed experimentally whether colonial breeding enhanced predator defence (by earlier detection, increased recruitment and/or overall higher efficacy of defence) and allowed individuals to decrease their investment in predator defence (either by decreasing the time spent in defence or their risk of injury from the predator). As risks for the mobber depend on the type of predator, we evaluated responses to two types of predators, those representing a direct risk for the mobber, and those that do not (but which represent a risk for the nest contents). We also evaluated whether recruitment is modulated through alarm calls, and whether individual investment (cost) in terms of defence and alarm calls was associated with breeding status, and thus with the potential benefits from the behaviour.

Methods

Study area and species

Fieldwork was conducted from 1994 to 1998 in four study areas: one near Madrid (central Spain, 40°30′ N, 3°30′ W) and three in Poitou-Charente (western France, 46° N, 0°30′ W). All nests were located (20–80 nests/year in each area) and their position was plotted on 1:10,000 scale maps. We used the number of neighbouring nests within a 600-m radius of each nest as a measure of nest density (see Arroyo 1995).

Nests were visited regularly to check clutch size and other breeding parameters. The date of laying of the first egg was back-dated from chick measurements (Brignon 1997). Montagu's harriers in their first year retain their juvenile primaries and characteristic uniform secondaries (Arroyo and King 1996). Most first-year birds (all males and >60% of females) do not breed (Arroyo 1996; Salamolard et al. 2000).

Experimental procedure

In each test, one of three different predator decoys (a plastic crow, four models; a plastic eagle owl, three models; or a stuffed fox, two models) was presented near a nest. Foxes and crows were common in all areas, both eat eggs and young, and foxes may kill adult harriers. Eagle owls did not breed within the study areas, but elsewhere eat Montagu's harrier nestlings and adults (B. Arroyo unpublished data). The eagle owl and fox are potentially dangerous for the adults, but the crow is not.

Decoys were placed when no birds were in flight or visible (>75% of cases), or whilst the observer was covered by a camouflage net. The outcome was observed at a distance from a hide or car. Foxes were placed on the ground, crows and owls on a 1-m-high perch. Each decoy was placed between 10 and 100 m from the nest (mean±SD 43±21 m, n=229). The distance depended on landscape and nest position within the field (decoys were usually placed in the nearest edge of the field). The average distance between non-isolated study nests was 228±163 m (n=86), so the decoy was always much closer to the nest of the tested pair than to neighbouring nests. Tested pairs were chosen for the ease of visibility and access, and where both pair members could be identified from wing-tags (20% of all birds) or individually identifiable plumage features (irregularities or anomalies in plumage, advanced moult, broken feathers, first-year plumage). In contrast, the origin of recruits (mobbers other than the tested pairs) could not always be determined. Overall, the proportion of tested pairs with no neighbours or breeding in small, medium-size or large colonies was similar to that observed in the study area (χ^2_3=5.17, P=0.16).

We considered the decoy as detected if a harrier flew within 100 m and approached it. In such cases, we noted detection time, detector sex and age (adult, fledgling or immature) and whether the detector was a member of the tested pair or another individual. We recorded the number, characteristics (sex, age, whether they were a member of the tested pair or not) and behaviour (time present, alarm calls and attacks) of all mobbers for 10–15 min after detection. Length of the tests after detection varied due to fieldwork constraints. If the decoy was not detected within 20 min, the trial was usually stopped and "no detection" was recorded. In some cases, however, we continued monitoring until detection to balance the sample size of individual behaviour after detection. Time until detection was unrelated to behaviour after detection in all the variables we tested.

Of a total of 229 tests on 120 different pairs, detection occurred in 133 tests by 92 different pairs. Of these 92 pairs, 59 were tested once, 26 twice and 7 three times, but no pair was tested more than once with the same predator type. For pairs that were tested more than once, the average interval between tests was 5±3 days (n=40). We had no indication that either habituation or sensitisation had occurred from previous exposure to a decoy. When considering all tests for the analysis of predator detection (i.e. including tests without detection), some pairs were tested more than once with the same decoy; to avoid pseudo-replication problems, we used only the first per pair of each decoy type.

Definition of variables and statistical analyses

Detection was positive if the decoy was detected within 20 min, negative otherwise, and we used this categorical variable for the analyses of detection.

Investment in defence after detection was measured for each individual using the following variables: (1) % time present (as a % of the length of the test after detection); (2) presence or absence

of an attack (i.e. a dive over the decoy), coded as 0 or 1; (3) attack rate, for individuals that engaged in attacks (number of dives per minute present); (4) % of risky attacks; i.e. the percentage of attacks when mobbers touched the decoy or their feet came within 50 cm of the decoy, as opposed to far-off dives (ending 0.5–3 m from the decoy), and (5) alarm rate (number of alarm calls per minute present). Alarm calls could not be quantified reliably in all tests (depending on wind conditions and distance to the observer), so sample sizes for alarm rates are smaller than those of the other variables measured.

Statistical analyses were performed with SAS 6.12 (SAS 1988). Means are expressed ±SD and all tests are two-tailed. Data were checked for normality and transformed where necessary (log transformation for frequencies, arcsine transformations for percentages). We used logistic regressions (CATMOD procedure, maximum likelihood analyses; SAS 1988) to estimate the impact of different factors or of their interactions on the probability of detection and the probability of attacking after detection. The initial models included all factors expected to affect the variable to be explained and all their interactions. The relative importance of each effect was analysed by removing them one at a time, beginning with interactions, from the initial model. For each effect removed, the increase in deviance was tested using χ^2 (the χ^2-value and degrees of freedom being obtained by the difference between the deviance and the degrees of freedom of the new and the previous models; Crawley 1993). This operation was conducted iteratively until the increase in deviance was no longer significant. In the results, we present the final models, i.e. the most parsimonious ones with the lowest Akaike Information Criterion values (SAS 1988).

The three types of decoy were considered separately for the analysis of detection, given that the fox was placed on the ground whereas other decoys were placed on a perch. However, overall there was no difference between responses against the fox and the owl after detection. Both represent a potential risk for adults, so we pooled tests with the fox and the owl, hereafter referred to as 'dangerous predators', for the analyses of response after detection. To evaluate breeding-stage effects, tests were classified a posteriori into three periods relative to calculated laying date (day 0): incubation (days 0–30), nestling (31–60) and post-fledging (60–90).

Distance between decoy and nest had no significant effect on either probability of detection, total attack rate or individual attack rate on the decoy. Similarly, the proportion of tests where only one or two members of the tested pairs were present did not vary with number of neighbours, number of other birds present, type of decoy or breeding stage. Consequently, these factors were not included in the models.

Results

Colonial breeding and predator defence enhancement

The chances of detection increased significantly with the number of neighbours (Fig. 1) and with breeding stage, from 30% (n=61) in the incubation period to 53% (n=95) in the nestling and 70% (n=23) in the post-fledging period. Decoy type and all the interactions were not significant and were excluded from the final model (Table 1).

After detection, the number of recruits (maximum eight) depended on the number of neighbours, and on the interaction of this variable and predator type (Table 2): the number of recruits increased with the number of neighbours in response to dangerous predators (linear regression: $F_{1,78}$=28.89, P<0.0001), but not to the crow ($F_{1,51}$=1.77, P=0.19; Fig. 2). The number of individuals attacking the decoy simultaneously increased with mobbing group size (linear regression: $F_{1,131}$=84.56,
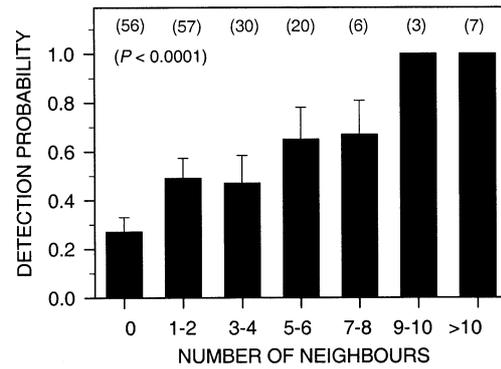

Fig. 1 Mean (±SE) probability of decoy detection in relation to the number of neighbours of tested pairs. Sample size (number of tests) is indicated above the histograms
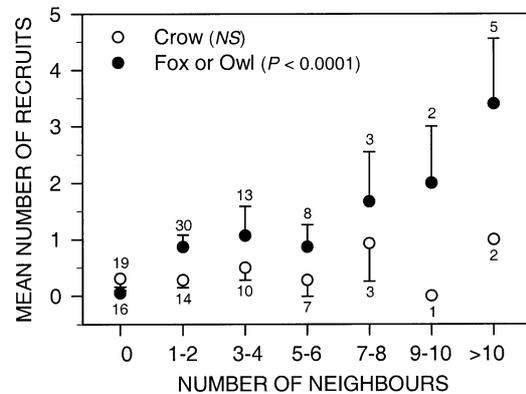

Fig. 2 Mean (±SE) number of individuals other than the tested birds recruited for defence, in relation to the type of decoy (*open circles* crow, *closed circles* fox or owl) and the number of neighbouring breeding pairs. Sample sizes refer to number of tests

Table 1 Results of the logistic regression testing for the effects of breeding stage (incubation, nestling, post-fledging), type of decoy (owl, fox, crow), number of neighbours and all their interactions on the probability that the decoy is detected. Only variables included in the final model are presented

Source	df	χ^2	P
Intercept	1	6.9	0.008
Number of neighbours	1	14.6	0.0001
Breeding stage	2	9.2	0.01
Likelihood ratio	24	24.6	0.43

Table 2 Results of the general-linear-model analysis on the effect of breeding stage (incubation, nestling, post-fledging), predator type (dangerous or non-dangerous) and number of neighbours (*NN*) on the number of individuals other than the tested birds recruited for defence (model: $F_{9,123}$=8.80, P=0.0001, r^2=0.39)

Source	df	F	P
Breeding stage	2	2.07	0.13
Predator type	1	0.02	0.89
NN	1	22.31	0.0001
NN×stage	2	1.87	0.15
NN×predator	1	6.50	0.012
Stage×predator	2	0.09	0.91
NN×stage×predator	2	0.25	0.78
Error	123		

Table 3 Average (±SD) anti-predator behaviours of different individual classes participating in defence [*n* sample size(number of individuals)]. Comparisons for time present, attack rate and per- centage of close dives are based on one-way ANOVA. Comparisons for percentage of individuals attacking and alarming are based on χ²-tests

	Tested individuals (a)	Other birds (b)				Comparisons a-b		Comparisons c-d	
		Breeders (c)	Non-breeders (d)	Fledglings	Unidentified	$F\chi^2$	P	$F\chi^2$	P
n	186	32	12	17	44				
Time present	86.9±25	46.6±35	31.7±23	34.7±22	29.2±27	201	0.0001	2.31	0.14
Percent individuals attacking	48	31	50	29	20	10.32	0.0001	1.32	0.25
Percent individuals alarming	61	41	25	47	32	15.7	0.0001	0.92	0.34
Attack rate	0.84±1.16	0.51±0.59	1.04±0.86	0.64±0.18	0.71±1.02	0.19	0.60	3.19	0.096
Percent close dives	55.8±42	50.0±53	27.8±64	0.00±0	42.0±46	1.93	0.17	0.82	0.38

P=0.0001), as well as the overall frequency of attacks (dives per minute) towards the decoy ($F_{1,131}$=16.3, P=0.0001).

Alarm calls and recruitment

The alarm rate of the tested individuals did not vary with either the number of neighbours or breeding stage, but was affected by the type of predator (ANCOVA: partial $F_{1,148}$=18.65, P=0.0001; all other variables or interactions not significant). Overall, alarm rate was higher for the fox or owl (2.13±3.35 calls/min, *n*=94 tests) than for the crow (0.32±1.00 calls/min, *n*=59). Similarly, initial detectors that were not members of the tested pairs alarmed more frequently for dangerous predators (57% of 14 cases) than for the crow (0% of 6 cases), although their alarm rate was lower (0.56±1.03 calls/min, n=8) than in tested individuals.

The number of birds recruited for defence increased significantly with increasing alarm rate of the tested individuals (Fig. 3), after controlling for colony size ($F_{1,98}$=25.61, P<0.0001). Moreover, the proportion of recruits engaging in attacks towards dangerous predators increased with the alarm rate of the tested birds (linear regression: $F_{1,20}$=7.64, P=0.012; Fig. 3). In contrast, the proportion of recruits attacking the crow was not related to the alarm rate of the tested birds ($F_{1,8}$=0.19, P=0.67).

Status and anti-predator behaviour of recruited birds

For all tests pooled, 105 individuals that were not members of the tested pairs participated in defence. Of these, 17 were fledglings either from the tested pairs or neighbouring pairs (distinguishing between them was not possible), 32 were identified as breeding neighbours, 12 as non-breeders and 44 were adult males and females of unidentified breeding status. Birds identified as neighbours come from nests up to 600 m away (mean 222±171 m, *n*=20 nests), and were generally the nearest (50% of cases) or second-nearest (35% of cases) neighbour.

Recruits were present for a shorter period of time and attacked and alarm called less often than the individuals
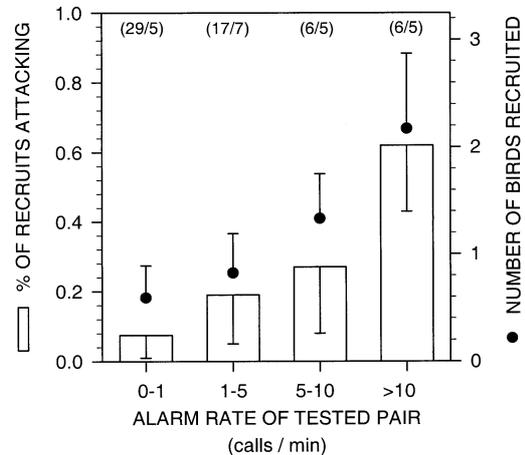

Fig. 3 Mean (±SE) number of birds recruited and mean (±SE) percentage of birds present that attacked dangerous predators in relation to the alarm rate of the tested pairs. Sample sizes above the histograms refer to number of tests/number of tests with recruits

from the tested pairs (Table 3). When engaged in attacks, however, they attacked at a similar rate to tested birds and with a similar proportion of close dives (Table 3). Among recruits, no significant differences were found in the investment in defence between breeders and non-breeders (Table 3).

Adjustment of individual behaviour according to recruitment

The behaviour of tested individuals varied according to the presence of other birds when confronted with potentially dangerous predators (fox or owl). First, the probability of attacking such predators increased with the number of other birds present (logistic regression: χ^2_1=7.40, P=0.006; Fig. 4); no other variables (breeding stage, number of members of the pair present, or their interactions) were retained in the final model. Second, the attack rate of lone birds was lower, but the percentage of close dives was higher, than when other birds were pres-
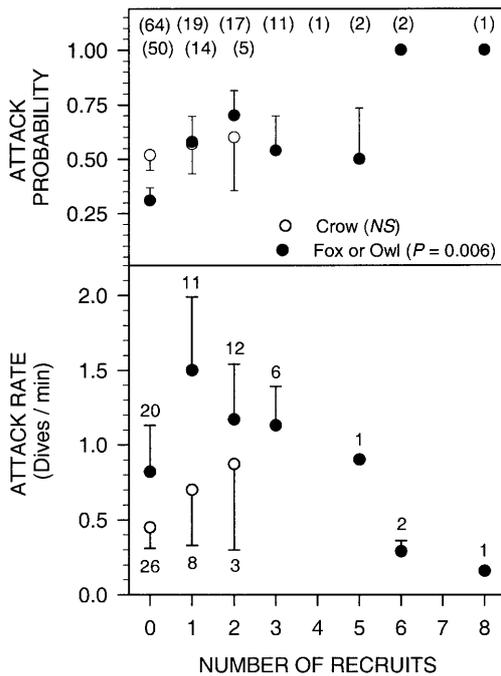
Fig. 4 Mean (±SE) probability of attack and individual attack rate of tested pair members that engaged in attacks in relation to the type of decoy (*open circles* crow, *closed circles* fox or owl) and to the number of other birds recruited for defence. Sample size refers to number of individuals
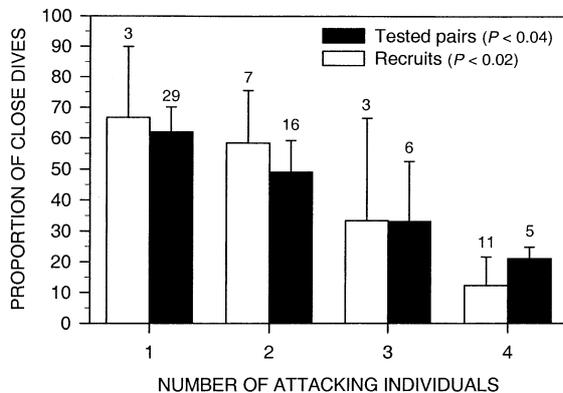

Fig. 5 Mean (±SE) percentage of close dives for each tested and recruited individual in relation to the number of individuals attacking dangerous predators. Sample size (number of individuals) is shown above the histograms

ent (one-way ANOVA: $F_{1,51}=4.97$, $P=0.033$; $F_{1,51}=4.20$, $P=0.046$, respectively). Overall, the percentage of close dives decreased significantly with the number of simultaneously attacking individuals ($F_{1,51}=4.51$, $P=0.038$; Fig. 5). Additionally, when recruits were present, there was a suggestion that individual attack rate decreased with increasing number of recruits (Fig. 4; linear regression, $F_{1,32}=2.45$, $P=0.12$).

In contrast, behaviour of the tested birds did not vary according to recruitment when confronted by the crow. The probability of attacking the crow was not related to any variable considered (breeding stage, number of birds present, or their interaction; logistic regression, $P>0.4$). Furthermore, neither attack rate nor the percentage of close dives varied significantly with the number of recruits (linear regression: $F_{1,35}=0.81$ and 0.48, respectively, $P>0.30$) or the number of attacking individuals (t-test, $t_{17}=1.76$ and 0.04, respectively, $P>0.10$).

Probability of attack in recruits did not depend on the number of individuals present (logistic regression, $P=0.6$), nor did attack rate vary with the size of the mobbing group ($F_{1,28}=0.08$, $P=0.8$). In contrast, and similar to the tested individuals, when confronted with a dangerous predator, the percentage of close dives decreased significantly with the number of simultaneously attacking individuals ($F_{1,22}=7.33$, $P=0.013$; Fig. 5).

Discussion

In Montagu's harrier, coloniality improved predator detection and was associated with more individuals recruited for defence. This in turn increased overall defence efficacy in terms of number of attacks on the predator. Thus, communal detection and defence could theoretically benefit Montagu's harriers breeding in colonies by reducing the probability of nest predation. Indeed, the predation rate was four times lower in colonial than in isolated nests in the Madrid study area (4 vs 15%; B. Arroyo, unpublished data). These results confirm the benefits of colonial breeding in terms of detection and active defence against predators (Bertram 1978; Brown and Brown 1996).

Communal defence, individual investment and risk acceptance

Increased recruitment for defence also influenced individual investment, mainly when attacking predators that represented a risk for adults. Risk acceptance is modulated by the relative costs and benefits of driving off the predator (Montgomerie and Weatherhead 1988; Redondo 1989): risks should only be accepted when the benefits are high, and the costs relatively low. Lack of mobbing behaviour towards dangerous predators occurs in many species, presumably due to the high risk of such behaviour and to the relatively low effectiveness of small species in deterring large predators (Elliot 1985a; Green et al. 1990). We have seen Montagu's harriers driving away crows, kites, dogs and foxes through mobbing, so deterrence of large predators occurs in this species. Nevertheless, the risk of injury from foxes or owls is potentially high. Montagu's harriers apparently adjusted their mobbing behaviour and risk acceptance according to the costs of such behaviour (type of predator) and the expected benefits (the probability of deterring the predator, evaluated from the total number of individuals recruited). As the size of the mobbing group increased, threatened parents were more likely to attack dangerous predators, but did so less intensively. Mobs provide 'selfish herd'

benefits (Hamilton 1971), which might explain the increased attack probability in groups: individuals can reduce their own risk when attacking in larger groups. Additionally, the effect of confusion to the predator when several mobbers are overhead has been shown for other species (Winkler 1992, 1994; Flasskamp 1994) and confirms that a higher number of attackers compensates for the lower individual attack intensity.

Colonial breeding in Montagu's harrier thus allows individuals to decrease the cost of defence in terms of risk taken, endorsing the results of previous interspecific studies (Brown and Hoogland 1986). This was achieved by increasing recruitment in situations where individual defence is inefficient or too costly (e.g. with a predator potentially dangerous for the adult). The possibility of mobbing dangerous predators at a reduced risk implies a high individual net benefit because it potentially increases adult survival, as well as reducing nest failure.

The relationship between colony size and benefits in terms of predator defence was not asymptotic, similar to results for lesser kestrels (Tella 1996) but in contrast to observations with gulls (Allainé 1991). This suggests that optimal colony sizes (with regard to defence at least) would be the largest. In contrast, colony sizes observed in this species show that medium sizes (four to seven pairs) are the commonest (authors, unpublished data). Optimal colony size for a given species depends on a number of factors, because different selective pressures can operate in different directions (Bertram 1978; Brown et al. 1990). For example, competition for food, interference or competition for nest sites or mates can be inversely related to colony size (Hoogland and Sherman 1976; Haas 1985; Wiklund and Andersson 1994; Brown and Brown 1996). Moreover, even when considering only predation-related factors, different types of predator or predation risk at different times of the breeding cycle might select for different dispersion patterns (Hogstad 1995; Brunton 1999). Coloniality in Montagu's harrier is associated with increased costs of mate guarding/paternity assurance (Arroyo 1999; Mougeot et al., 2001), and possibly increased competition for food (Arroyo 1995). Ultimately, optimal colony size might vary for each individual, as individual quality might also influence individual net gain in different group sizes (Brown et al. 1990).

Investment of recruits: mutual benefits or manipulation?

Whether communal mobbing is a selfish or altruistic trait has long been questioned (Shields 1984). Communal defence might be based on the gain of mutual benefits (Trivers 1971). Potential benefits for the recruits range from self-defence, defence of own offspring or information gathering (Curio 1978; Winkler 1994). Self-defence is unlikely to explain Montagu's harrier behaviour. Although the fox and the owl are potentially dangerous, the probability of predation of adults is very low, and potential self-defence benefits probably do not compensate for the engagement in mobbing. Conversely, benefits related to defence of young and information/experience gathering could help explain participation in defence by neighbouring breeders and unexperienced birds. The clearest benefit in group defence was for the non-tested neighbouring breeders (see also Shields 1984; Winkler 1994), which formed an important proportion of all birds recruited. Additionally, communal defence could be related to gathering information on predators (Curio 1978; McLean et al. 1986), as suggested in our study by the presence of passive recruits (those that do not alarm or attack). Furthermore, the participation of fledglings in communal defence may lead to cultural transmission of enemy recognition (see Curio et al. 1978; Conover 1987). Learning which predators are more dangerous through the behaviour of other individuals may be important, since preliminary experiments suggest that fledglings reared in captivity did not recognise owl decoys as predators (F. Mougeot and B. Arroyo, personal observations).

Nonetheless, 11% of recruits were identified as non-breeders. Furthermore, recruits of non-identified status behaved in a manner intermediate between breeders and non-breeders (Table 3), suggesting that they included at least some non-breeders. Non-breeders invested as much in defence as did other recruits. This behaviour might be based on the anticipation of future benefits such as increased probability of future reproduction, although this is unlikely as individuals are not faithful to their breeding places from year to year in this species. Therefore, the participation of non-breeders in defence suggests that there is an asymmetry in the distribution of the benefits gained, and that investment of recruits might partly be the result of exploitation by the tested pairs (Krebs and Dawkins 1984). Both the number of individuals recruited and the probability of attack by the recruits were modulated by the alarm calls of the tested pair, which were in turn adjusted to the risk that the predator represented for the mobbers. Tested birds used higher alarm rates when confronted with a dangerous predator, possibly to manipulate the behaviour of other birds, make them approach (thus increasing the efficacy of the defence) and ultimately make them attack the predator (thus decreasing their own risk). Recruitment, therefore, mainly benefited the tested birds, i.e. those most threatened by the presence of the predator. Manipulative behaviour may be maintained by the gain of some benefits for the reactor (Krebs and Davies 1993). In Montagu's harrier, the potential benefits to recruits (information about the predator or, for the neighbouring birds, defence of their own offspring), might be sufficiently important to maintain (reciprocal) manipulation by breeding birds.

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