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Woodpigeons nesting in association with hobby falcons: advantages and choice rules

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Many bird species nest in close association with other bolder and more aggressive birds which provide protection against nest predators. The woodpigeons, *Columba palumbus*, that nest in poplar plantations in Northern Italy are found almost exclusively clumped around hobby, *Falco subbuteo*, nests. Woodpigeons settle in the area and build their nests after the hobby has started nesting. We carried out experiments with dummy nests and observations on woodpigeon nests. Dummy woodpigeon nests placed near a hobby's nest suffered less depredation by hooded crows, *Corvus corone cornix*, than those placed far from it. A logistic regression analysis showed that three variables, hobby nesting stage, distance from the hobby's nest and the hobby's aggressiveness, influenced the probability of nest predation. The degree of protection varied during the hobby's nesting period and was highest when chicks were in the nest. The hobby's aggressiveness against intruders varied both between and within individuals during different nesting phases. The predation rate of dummy nests associated with the falcon was negatively correlated with the aggressiveness score of the hobby during the 6 days of dummy nest exposure. Observations on real nests showed that woodpigeons selected hobbies that had a high fledging success, and a more vigorous defensive behaviour. Clues that would allow woodpigeons to choose the best protector may be early nesting by the hobby and its aggressiveness. Hobbies preyed on adult woodpigeons, but the risk incurred by the woodpigeons was low compared with the very high risk of nest predation in this area.

Predation is the main cause of nesting failure in birds and the most important component of egg and chick mortality (Ricklefs 1969; Martin 1993). As a result, the probability of nest predation plays a key role in regulating nesting chronology, habitat selection and life-history traits (Martin 1992). Among the traits that probably evolved under the pressure of nest predation is the association between 'timid' and 'formidable' species (Collias & Collias 1984), capable of keeping potential nest predators out of their nest area (e.g. Wiklund 1979, 1982).

Many bird species have been observed nesting in association with more aggressive birds (e.g. Durango 1949; Clark & Robertson 1979; Wiklund 1979; Dyrcz et al. 1981; Norrdahl et al. 1995) or with stinging insects (Joyce 1993; Dejan & Fotso 1995). Two mechanisms of predation reduction have been suggested: (1) the aggressive species maintains an area around its nest free of nest predators, so the associated species benefits from a 'protective umbrella' (Dyrcz et al. 1981); and (2) the aggressive species gives an early alarm when predators are approaching, so that the associated birds have time to cover the nests and to hide; this is the 'information parasitism' hypothesis proposed by Burger (1984). The association may be beneficial to both species if the timid species joins the bolder one during mobbing or if it contributes to early warning when the potential predator is approaching (Wiklund 1979, 1982). The aggressive species may also benefit from the dilution effect against nest predation provided by other nests in the surroundings (Clark & Robertson 1979). Furthermore, when faced with a choice, a predator capable of preying on the nest of both species is expected to attack the timid one, with which the risk of injury is lower. In many cases, however, the association seems to confer an advantage on the timid species only (e.g. Dyrcz et al. 1981); in this case the breeding association can evolve only if it is not costly to the aggressive species.

The association of timid species with a diurnal raptor has been frequently reported, but the advantage for the timid species has been shown in only a few cases (e.g. Wiklund 1982; Bijlsma 1984; Ueta 1994; Blanco & Tella 1997). In this paper we describe the association between two species: the hobby, *Falco subbuteo*, and the woodpigeon, *Columba palumbus*, which have been

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observed nesting close to one another in various parts of their breeding range (e.g. Collar 1978; Bijlsma 1984). Our study area had a particularly homogeneous habitat structure; habitat variables could therefore be easily controlled and we could exclude the possibilities that the nesting association was the result of an independent choice of the same habitat features, or that suitable habitat was scarce and limiting (Bogliani et al. 1992). In our study area both species occurred in the same woodlots, where woodpigeon nests were clumped around hobby nests; the hobby, but not the woodpigeon, is very active against all potential nest predators within the nest area and can therefore be classified as the more aggressive species (Bogliani et al. 1992). We considered the following questions. (1) Do both or one of the species benefit from the association? (2) Among the hobbies, are all pairs equally effective in protecting the nests of the associated species? (3) Do woodpigeons associate more frequently with hobbies whose behaviour correlates positively with woodpigeon nest survival? (4) What are the clues that permit the woodpigeon to forecast the protective tendency and ability of the hobby pair with which it associates? (5) Does the woodpigeon incur any risk in associating with the falcon?

METHODS

Study Area

We studied hobbies and woodpigeons nesting in a 40-km stretch of the seasonal flood plain of the Po, Italy (45°N, 9°E). The study area covers 62 km^2, of which over 20 km^2 are poplar, *Populus* × cultivar, plantations. The majority of the poplars belong to a single clone (I-214). The trees are planted in a quadrate design, 5–6 m apart at a density of 320–350 trees/ha. The ground is harrowed at least twice a year during the first 4 years and thereafter only once a year. The trees are usually felled at the age of 10 years, seldom at 11 or 12 years. Other wooded areas include mainly hedgerows, copses of willows, *Salix alba*, close to the river and false-acacia, *Robinia pseudoacacia*, on drier soils. The nonwooded areas are intensively cultivated with maize, wheat and soybean. For further details see Bracco et al. (1984) and Bogliani et al. (1994a).

Study Population

Nests of hobbies were regularly spaced at a high density (23.9 breeding pairs/100 km^2: Bogliani et al. 1994b). The distance to the nearest neighbouring nest was 1798 ± 906 m ($\bar{X}$ ± SD; N=89). Breeding success was similar to that of other European populations with, on average, 1.8 fledged young per reproductive pair (N=78). Only old hooded crow, *Corvus corone cornix*, nests were used by the hobby as nesting sites. Among available crow nests, hobbies selected those on more mature trees (Sergio & Bogliani 1995).

Woodpigeons breeding in the study area nested almost exclusively in poplar plantations. A careful search in other habitats led to the discovery of very few nests. Moreover, a census carried out by mapping territorial displays, such as territorial flights and vocalizations, indicated breeding woodpigeons only in poplar plantations (Bogliani 1988). Woodpigeon nests near hobby nests were conspicuous and could be seen from as far as 50 m, while those far from the hobby seemed to be hidden among the foliage.

Experiments with Dummy Nests

We built dummy woodpigeon nests by fixing a square of weathered chicken wire net (20 × 20 cm) to a poplar branch close to the trunk. The net supported an imitation woodpigeon nest 15 cm in diameter, made of woven twigs and dry grass. Two domestic quail, *Coturnix japonica*, eggs were placed in the nest. To simulate typical white woodpigeon eggs, we soaked the quail eggs in vinegar for 15 min and then rubbed them under tap water, to remove the shell pigment. The mean weight of the quail eggs was 15 g; woodpigeon eggs weigh 19 g (Cramp 1985). Between 1992 and 1994, we placed two sets of five dummy nests around each of 20 hobby pairs; the first set was positioned within 50 m of the falcon's nest and the second further than 100 m from it. The two sets of dummy nests were always placed as near as possible to each other so as to be included as far as possible in the same predator's home range. When possible, we placed the two sets in the same plantation or, when in different woodlots, we placed them in plantations of the same age, so as to standardize all the vegetation structure variables potentially influencing predation rates. We checked dummy nest predation, defined as at least one egg stolen or damaged after 6 days of exposure. The experiment was carried out twice around 19 hobby nests and once around one nest, giving a total of 39 replicates; at least 15 days were left between the end of one replicate of the experiment and the beginning of the next in the same nest, to avoid habituating the local predators. We never used the same hobby territory in consecutive years, so as to minimize the probability of testing the same pairs twice. Owing to a small sample size, replicates of the experiments carried out during the second part of the postfledging period were analysed separately from other data.

Behaviour of the Hobby at the Nest

Incubating hobbies were classified as tight-sitters if, during incubation, they remained on the nest when the observer approached as close as 1 m to the nest tree, or as loose-sitters if they abandoned the nest. Every time a nest was visited, we recorded the behaviour of the female and scored it as follows: (1) flushes and disappears; (2) flies high above the nest area and does not vocalize; (3) flies high and gives four or fewer alarm calls; (4) flies high and gives more than four alarm calls; (5) as in (4), but also stoops towards the intruder, remaining above the canopy; (6) flies among the trees, more than 50 m from the intruder, then perches and calls; (7) as above, but flies closer than 50 m to the intruder; (8) makes several close stoops towards the intruder, continually uttering loud cries. This behaviour was almost exclusively observed in the female; the male, distinguished by his smaller size, was frequently observed flying high above the canopy, seldom calling and then only at low intensity.

Between 1992 and 1994 we classified the nest defence behaviour of 40 female hobbies against a human intruder according to an aggressiveness score (F. Sergio & G. Bogliani, unpublished data). We sampled females during four phases of the breeding cycle: incubation; nestlings younger than 15 days; nestlings older than 15 days; postfledging. We analysed the data with nonparametric tests (Siegel & Castellan 1988). We also tried to measure the rate of aggression towards real avian intruders as in Ueta (1994), but the hobby attack rate was too low to allow any data analysis. During 50 h of nest watching during 1994, 65 individuals of seven species during incubation and 103 individuals of four species during chick rearing were seen flying within a 50-m radius of six hobby nests; 73.8% of intruders were hooded crows. Only four attacks were observed, all involving the latter species.

Hobby Nest Contents

We calculated hobby productivity only for nests found during egg laying or incubation. We inspected nests at least three times: during incubation, a few days after hatching; and when the chicks were nearly ready to leave the nest. We used a mirror fixed on an extendable pole 23 m high, or directly climbed the nest tree. Each inspection generally lasted less than 5–10 min. The number of eggs was determined as the number observed during incubation or as the number of chicks aged less than 10 days plus the unhatched eggs, as in Fiuczynski & Nethersole-Thompson (1980). We determined the laying date of the first egg by counting 30 days back from the hatching date of the first chick (Cramp & Simmons 1980).

Hobby Diet

We collected pluckings and prey remains under hobby nests on each visit during 1992–1994. Prey identification was based on comparison with a reference collection.

Data Analysis

Data were tested for normality and log transformed or arcsine square-root transformed as necessary. Predation rates of dummy nests were always arcsine square-root transformed for any parametric test; other data transformations are specified in the Results. If no adequate transformation was found, we used nonparametric tests. All P values are two-tailed; statistical significance was set at α=0.05. When multiple comparisons were carried out on a set of values, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989).

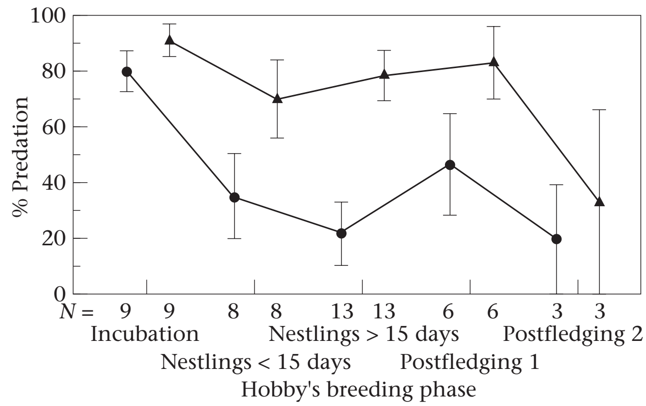

Figure 1. Percentage of dummy woodpigeon nests that were preyed on ± SE, for nests set within 50 m of a hobby's nest (●) and set more than 100 m from a hobby's nest (▲) during different phases of the hobby's breeding season. Postfledging 1 indicates the first 10 days after fledging; postfledging 2 indicates days 11+ after fledging.

Problems could arise by treating artificial nests as independent units, as dummy nests were set in groups of five near and away from each hobby nest. We avoided the 'pooling fallacy' (Machlis et al. 1985), however, by using an equal number of dummy nests around each hobby nest (Leger & Didrichsons 1994).

RESULTS

Dummy Nest Predation

The percentage of dummy nests close to hobby nests that were preyed on varied through the hobby's breeding period (data grouped as in Fig. 1, but postfledging 2 not included in the analysis; $F_{3,32}$=4.33, P=0.01). A post hoc comparison with the Duncan test at P<0.05 showed that the incubation period differed from the first half and the second half of the period with chicks in the nest. A similar analysis carried out on dummy nests far from hobby nests showed no significant difference between breeding stages ($F_{3,32}$=0.25, P=0.86).

Dummy nests close to hobby nests were preyed on less than those far from the hobby (Fig. 1). The difference in predation between the two sets was significant when the hobbies had chicks more than 15 days old (t_{12}=5.02, P<0.01). No significant difference was observed during incubation, when chicks were less than 15 days old, and during the postfledging period (second part of postfledging: Fisher's exact test: P=0.68). The effect of the distance from the hobby was also evident when only dummy nests within 50 m were taken into account. In this case, the percentage of nests preyed on correlated positively with the distance from the hobby (r=0.32, N=37, P=0.05; Fig. 2).

In a stepwise logistic regression analysis carried out on all dummy nests (N=360), using as a dependent variable the predation or survival of each nest and as independent variables those shown in Table 1, both the distance from the hobby and the reproductive phase of the hobby entered the model. The model correctly classified 87% of

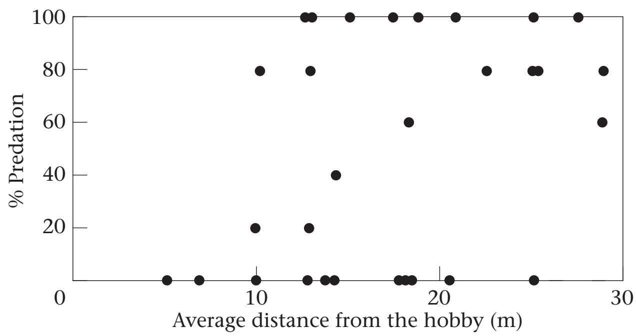

Figure 2. Percentage of dummy woodpigeon nests set within 50 m of a hobby's nest that were preyed on, as a function of the distance from the falcon's nest.

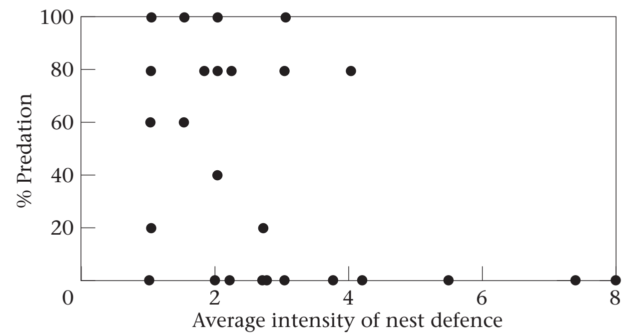

Figure 3. Percentage of dummy woodpigeon nests set within 50 m of a hobby's nest that were preyed on, as a function of the aggressiveness score of the falcon.

depredated dummy nests and 61% of nondepredated nests; overall, we correctly classified 77% of cases.

The pattern of predation was also different between the two groups of dummy woodpigeon nests; in a significantly higher proportion of dummy nests near hobby nests, predation involved only one of the two eggs (18 versus 5%, N=83; Fisher's exact test: P=0.05), whereas in dummy nests far from hobby nests the proportion of complete clutch depredation was more frequent.

Hobby Nest Defence

Some hobby females were more aggressive than others and their behaviour was consistent throughout the breeding season; there was a significant positive correlation between the aggressiveness scores of the same female tested twice during the nesting season (Spearman rank correlations: incubation/postfledging: r_S=0.56, N=17, P=0.019; incubation/nestlings older than 15 days: r_S=0.46, N=27, P=0.015; nestlings older than 15 days/postfledging: r_S=0.78, N=19, P<0.001). Intensity of nest defence by male and female hobbies increased linearly from incubation to postfledging; female level of defence was positively correlated with brood size (F. Sergio & G. Bogliani, unpublished data).

Effect of Hobby Behaviour on Dummy Nest Predation

The percentage of dummy nests within 50 m of the hobby nest that were preyed on was negatively correlated with the aggressiveness score of the falcon during the 6 days of dummy nest exposure (Spearman rank correlation: $r_S = -0.53$, N=37, P=0.001; Fig. 3). To control for possible confusion because of intercorrelation between variables, we did a logistic regression analysis on dummy nest predation within 50 m of the hobby, using all variables that had an effect on nest predation rate if considered singly: distance from the hobby nest; reproductive phase of the hobby; aggressiveness score of the hobby, distance from the wood edge; and number of real woodpigeon nests within 50 m. The first three variables entered the model (Table 2). The model correctly classified 76% of depredated nests and 81% of nondepredated nests; overall, 79% of nests were correctly classified. A logistic regression analysis carried out with the same set of data, but without taking into account the aggressiveness of the hobby, gave a correct classification of 65% of depredated nests and 83% of nondepredated nests; overall 76% of nests were classified correctly. Therefore, the aggressiveness of the hobby, alone, enhanced the classification power of the logistic model by 11% for depredated nests and reduced it by 2% for nondepredated

Table 1. Logistic regression model of dummy woodpigeon nest predation

Variable	*B*	Wald statistic	*R*	*df*	*P*
Distance from the hobby nest*	−0.69	55.04	0.33	1	<0.001
Nesting phase of the hobby		38.18	0.24	5	<0.001
Constant		25.48		1	<0.001

Variables not entering the model: (1) number of real woodpigeon nests within 50 m; (2) distance from the wood edge. The dependent variable is the survival of the dummy nest until and including the sixth day of exposure. Dummy nests considered are within 50 m of the hobby nest or more than 100 m from it (N=360). Reproductive phase of the hobby was entered as a dummy variable. *B* is the estimated logistic regression coefficient (Norusis 1992).

*Variable log transformed.

Table 2. Logistic regression model of dummy woodpigeon nest predation of the sample set within 50 m of the hobby nest (*N*=180)

Variable	*B*	Wald statistic	*R*	*df*	*P*
Aggressiveness score of the hobby*	2.20	19.06	0.26	1	<0.001
Nesting phase of the hobby		21.84	0.22	5	<0.001
Distance from the hobby nest†	−1.05	9.37	−0.17	1	<0.01
Constant		0.09		1	NS

Variables not entering the model: (1) number of real woodpigeon nests within 50 m; (2) distance from the wood edge. The dependent variable is the survival of the dummy nest until and including the sixth day of exposure. Reproductive phase of the hobby was entered as a dummy variable.
*Variable square-root transformed.
†Variable log transformed.

nests; aggressiveness enhanced the model by 3%. Nests at more than 100 m from the hobby were not included in the analysis because we did not have aggressiveness data for this sample.

Selection of Woodlots by the Two Species

Different predation rates between dummy nests placed near and far from the hobby may also be caused by the falcon selecting poplar plantations with a low predation pressure, independently of the falcon's nest defence behaviour, in this case the clumping of real woodpigeon nests around each hobby nest could be caused by independent, contemporary selection of low predation woodlots by the two species. Whenever the two sets of dummy nests were placed in different plantations, however, there was no difference in density of hooded crows (nests/ha) between woodlots containing the hobby set and woodlots containing the control set (2.5 ± 0.7 and 2.5 ± 0.7, respectively; Wilcoxon signed-ranks test: $Z = -0.28$, $N=8$, $P=0.78$); we assume that the density of crow nests in a woodlot is a rough estimate of potential predation pressure in the woodlot. In addition, the percentage of dummy nests preyed on near the hobby was still significantly lower than that of dummy nests of the control set even in those 12 cases in which two sets had been positioned in the same woodlot (46 ± 9.4 and 7.6 ± 7.1, respectively; Wilcoxon signed-ranks test: $Z = -3.11$, $N=23$, $P=0.0019$). Finally, in case hobby pairs could detect variations in potential predation pressure within the nesting woodlot, which is unlikely, and consequently select low-predation areas within the plantation, we compared the number of hooded crow nests within 100 m of each set of dummy nests placed close to the hobby with that within 100 m of each control set: there was no significant difference (1.4 ± 0.2 and 1.5 ± 0.2, respectively; Wilcoxon signed-ranks test: $Z=0.31$, $N=20$, $P=0.75$).

Although not conclusive, these data show that observed differences in predation rates between the two sets of dummy nests cannot be explained in terms of initial selection of low-predation plantations by the falcon and that the observed differences still held when the two sets were placed in the same woodlot.

Observations on Real Woodpigeon Nests

We searched poplar plots suitable for the hobby for both falcon and woodpigeon nests. Out of 222 searched plots, 50 had woodpigeon nests but only three did not simultaneously host the hobby; the woodpigeon was present in 47 of the 77 plots with hobby nests checked in 1987, 1988 and 1992–1995 ($\chi^2_1=96.87$, $P<0.00001$). Within plots occupied by the falcon, woodpigeon nests were strongly clumped around hobby nests.

In a sample of 24 nests, the woodpigeon laying date could be determined: 71% of the clutches were started when the associated hobby was incubating and 25% when the hobby had chicks less than 15 days old. We observed no nest defence by the woodpigeon; adults invariably fled from the nest while the intruder was approaching.

The number of real woodpigeon nests around the hobby varied from zero to six ($\bar{X} \pm SD=1.1 \pm 0.14$, $N=50$); 65% of 50 hobby nests and 76% of 41 successful hobby nests had at least one woodpigeon nest within 50 m. On average, around hobby nests whose incubating female was classified as a tight-sitter there were more woodpigeon nests (1.1 ± 0.86, $N=13$) than around nests with loose-sitters (0.4 ± 0.60, $N=21$; $t_{32}=2.59$, $P=0.014$). Tight-sitters laid larger clutches (2.82 ± 0.4, $N=11$ versus 2.3 ± 0.7, $N=10$; $t_{19}=2.16$, $P=0.04$) and fledged more young (2.6 ± 0.5, $N=9$ versus 1.2 ± 1.2, $N=22$; $t_{29}=3.33$, $P<0.001$) than loose-sitters. The number of woodpigeon nests correlated positively with the fledging success of the associated hobby pair (Spearman rank correlation: $r_S=0.30$, $N=74$, $P=0.01$) but not with its clutch size (Spearman rank correlation: $r_S=0.15$, $N=39$, $P=0.36$). The number of woodpigeon nests also correlated negatively with the laying date of the associated hobby (Spearman rank correlation: $r_S=-0.33$, $N=49$, $P=0.011$, one-tailed test). The correlation between the number of woodpigeon nests and the hobby's laying date was no longer significant, but a tendency remained, after controlling with partial correlation analysis for intercorrelation between the fledging success and the laying date of the hobby nests ($r=-0.24$, $N=49$, $P=0.08$).

The Woodpigeon as Prey of the Hobby

Out of 317 identified bird prey individuals, 53% were common swifts, *Apus apus*, and 25% were sparrows, *Passer domesticus italiae* and *Passer montanus*; there were five woodpigeons (1.6%), and five domestic pigeons, *Columba livia*. In biomass, out of 15 798 g (fresh weight), 46% was formed by the common swift, 15% by woodpigeon, 13% by sparrows and 8.5% by domestic pigeons; the remaining 17.5% was represented by 15 species. Of individual prey (N=317) 89% had a mean weight of 20–50 g. Four out of five woodpigeon remains were found in the immediate surroundings of the hobby nest and, since their weight prevents the falcon from carrying them far, they were probably captured on site.

DISCUSSION

Artificial woodpigeon nests were preyed on less if they were associated with a hobby nest. The lower dummy nest predation near the falcon did not seem to be caused by selection of low predation areas for nesting by the hobby. Potential predation pressure, expressed as the density of hooded crow nests, did not differ between the woodlots containing the two sets of dummy nests, nor between the areas within 100 m of each of the two sets. Also, the predation rate of dummy nests near the hobby was still significantly lower than that of dummy nests of the control set, even considering only the cases in which the two sets had been positioned within the same woodlot. In addition, the two sets of dummy nests were always positioned so as to be subject as much as possible to the same predation pressure (see Methods) and temporal variations in predation rate of one set were parallel and positively correlated with variations in the other set (r_S=0.41, N=39, P<0.01). The only difference between the two sets was the amount of predation suffered, and the only factor that could explain such a difference is the presence of the hobby and its nest defence behaviour near the dummy nests. Even within the group of nests associated with a falcon, the percentage of nests preyed on correlated with the distance from the hobby. The distribution of real woodpigeon nests in poplar plantations also showed that this species selected for closeness to the hobby (Bogliani et al. 1992); overselection by the woodpigeon for trees within 20 m of a hobby's nest was also shown by Bijlsma (1984). The pattern of predation was also different between the two groups of artificial woodpigeon nests: predation of both eggs was more frequent for nests placed far from hobby nests whereas nests near hobby nests were more likely to lose a single egg, suggesting that, if the hobby was nearby, nest predators were less likely to discover or to reach the artificial nest. Although we cannot completely discount that independent selection of low-predation areas by the two species could at least partially produce the association, we suggest that the antipredatory advantages for the woodpigeon, caused by the nest defence behaviour of the falcon, are the main benefits favouring the evolution and maintenance of the association.

The effectiveness of the protection offered by the hobby varied throughout the falcon's breeding period in a manner related to the intensity of its nest defence. The dummy nests survived best when the hobby nest contained chicks or after fledging, when the young and their parents were still near the nest. In this period the intensity of nest defence by the falcon is also at a maximum (F. Sergio & G. Bogliani, unpublished data). During incubation, the female hobby showed less propensity to attack human intruders and tended to remain on the nest; the dummy nests were therefore more vulnerable to predation and no difference in survival rate between nests near and far from hobby nests was detected. After the hobby family left the nest area, the predation rate on all dummy nests was low. This could be because, in this period, young hooded crows suddenly dispersed from their nesting area and adult crows abandoned the poplar plantations and formed flocks in open habitats (Bogliani et al. 1994b). A similar pattern of temporal variation in nest predation was observed by Ueta (1994) on artificial azure-winged magpie, *Cyanopica cyana*, nests, associated with the Japanese sparrowhawk, *Accipiter gularis*, but with a major difference during incubation. At that time, the protective effect of the sparrowhawk was as great as during chick rearing; perhaps because, in this species, the male also takes part in nest defence (M. Ueta, personal communication), whereas, in the hobby, it is mainly the female that both incubates and defends the nest against heterospecific intruders (Nethersole-Thompson, in Cramp & Simmons 1980, pp. 321–322).

The rate of predation on dummy nests varied between hobby nests. Some hobby pairs were consistently more effective than others in keeping nest predators away and a correlation between aggressiveness scores by the same hobby during different phases of the breeding cycle was evident. The predation rate of dummy woodpigeon nests was negatively correlated with the intensity of nest defence by the hobby. Results of the second logistic regression showed that aggressiveness and reproductive phase of the hobby and the distance of the dummy nests from the hobby's nest all had an effect on predation probability (Table 2). Thus, observed patterns of dummy nest predation were always related to spatiotemporal variations of the intensity of nest defence by the hobby. It would be advantageous for the woodpigeon to associate with very aggressive hobby pairs; these are pairs with clutches and broods of high reproductive value. Our findings support such a prediction. The number of real woodpigeon nests around the hobby nests varied greatly and hobby pairs that fledged more young were associated with more woodpigeon nests. Therefore, woodpigeons seemed able to select hobby pairs with the best breeding performance, which also defended their nests more effectively. Hobby females defended more vigorously when tending broods of three than broods of two nestlings, for example. How the woodpigeon can assess nest defence behaviour of the hobby with which it will associate is not so clear. A possible rule of thumb used by the woodpigeon could be that hobbies nesting earlier and defending more vigorously during the early breeding phases will be more successful, thus continuing their protective effect throughout the woodpigeon's breeding period; these hobbies will also be more aggressive later on, thus keeping nest predators away from the nest area more efficiently. The woodpigeon also exploited the falcon's nest defence behaviour by synchronizing the most dangerous phases of its breeding cycle, that is, the period when the chicks are left alone in the nest, with the period of maximum aggressiveness by the hobby.

Associating with an aggressive predator could be risky for a species such as the woodpigeon, as adult woodpigeons were vulnerable to predation by the falcon. Nevertheless, the benefits of enhanced nesting success could well balance the potential costs of the association in an area where nest predators are so abundant.

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