Nest Defense as Parental Care in the Northern Hobby (*Falco subbuteo*)

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ABSTRACT.—Intensity of nest defense against a human intruder was recorded for 42 male and 43 female Northern Hobbies (*Falco subbuteo*) from 1992 to 1994. Defense did not vary between repeatedly and rarely visited nests. Except during incubation, intensity of nest defense by females was higher than that by males. For both sexes, defense intensity increased from incubation to fledging, within the nestling stage, and from fledging to the first 10 days of the postfledging period. Intensity of nest defense was positively correlated with brood size in females, but not in males. Experiments with dummy nests showed that defense was effective in deterring nest predation, and that its effect was positively related to its intensity. Hobby nest defense was an individually varying "plastic" trait, probably tuned to the reproductive value of the offspring. Parents apparently trade off the costs and risks of the behavior against the increasing likelihood of offspring survival.

Nest defense is an individually variable component of parental investment (Montgomerie and Weatherhead 1988). "Parental investment" is defined as any investment by the parent in an individual offspring that increases the offspring's probability of survival at the cost of the parent's ability to invest in other offspring (Trivers 1972). The cost involved in nest defense includes risk of injury or death of the parent, time and energy lost in defense, and risk of attracting additional predators (McLean et al. 1986). Parental investment theory predicts an increase in intensity of defense during the breeding cycle and with increasing brood size (Winkler 1987, Redondo 1989). Intensity of defense progressively increases during a breeding attempt because of an increase in cumulative past effort (but see Maynard Smith 1977), a progressive increase in expected fitness benefits (Knight and Temple 1986a, Winkler 1987), a decreasing ratio between the survival probabilities of the parents and those of their offspring (Andersson et al. 1980), a decrease in parental renesting potential (Biermann and Robertson 1981), or an increase in vulnerability and conspicuousness of the nestlings (Harvey and Greenwood 1978). Knight and Temple (1986b) have argued that the reported increase could

be a methodological artifact caused by positive reinforcement in repeatedly visited parents.

Here, we (1) examine sexual differences in the intensity of nest defense by a small falcon, the Northern Hobby (*Falco subbuteo*); (2) analyze variations in intensity of defense in relation to breeding stage, clutch size, brood size, and renesting potential; (3) test effectiveness of nest defense in reducing nest predation by means of an experimental approach; and (4) test Knight and Temple's (1986b) revisitation hypothesis.

Study area and Methods. The study area was along a 45 km stretch of the Po River (45°N, 9°E) in northern Italy (see Sergio and Bogliani 1999, 2000 for details).

Data on nest defense were collected during 1992–1994. We censused 16 hobby nests in 1992, 16 in 1993 and 14 in 1994. Intensity of nest defense was recorded by simulating a predation attempt by a human. During each trial, the predator positioned himself at a point 50 m from the hobby nest. The observer then walked slowly towards the nest. Once under the nest, he recorded the behavior of the adults for 5 min. Intensity of defense was quantified according to the following aggressiveness scores: (1) flies away and disappears; (2) circles silently high above the canopy; (3) circles high above the canopy and emits a few alarm calls (≤4); (4) circles high above the canopy and emits numerous alarm calls (>4); (5) as above, but with some shallow dips at the intruder; (6) flies away (>50 m) from the observer in the woodlot in a zig-zag path, then perches on a tree and gives continuous alarm calls (if the observer approaches, the hobby flies away); (7) as above, but nearer to the observer (<50 m); if the observer approaches closely, the hobby remains perched and continues to call; (8) stoops closely at the intruder. Progressive increases in score are associated with increases in energy costly activities, such as alarm calling, flapping flight and stooping, and with a decrease in distance from the potential predator, that is, with higher costs and risks for the defender. During incubation, we also classified incubating females as loose- or tight-sitters, depending on whether they fled when approached by the observer, or whether they remained crouched over the clutch in a flattened posture. Tight sitting was considered the more extreme form of defense because it allowed closer approach by the predator. Only cases in which both partners were observed near the nest since the beginning of the trial were included in the analyses of sexual differences in defense.

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"Dummy" nests, consisting of an open cup nest built by weaving twigs and dry grass and positioned on a quadrant of weathered chicken wire tied to the base of a poplar branch, were used to test the hypothesis that nest defense can be effective in reducing nest predation (Major and Kendall 1996). Two quail (*Coturnix japonica*) eggs were placed in each dummy nest (Bogliani et al. 1999). Between 1992 and 1994, two sets of dummy nests were placed around each of 20 hobby nests. Each of the two sets was composed of five dummy nests. The first set was placed within 50 m of the hobby nest, and the second (control set) further than 100 m from it. Predation or survival of each dummy nest and intensity of defense of the hobby were recorded every two days until the sixth day of exposure. A nest was classified as predated when at least one of the eggs was missing or broken. Each six day trial is defined as an experiment. Experiments were carried out during different stages of the hobby breeding cycle ($n = 39$ experiments).

Data were collected for 42 males and 43 females. The hobby breeding cycle was divided into five stages: (1) incubation; (2) nestlings ≤15 days; (3) nestlings > 15 days; (4) postfledging 1: within 10 days of the first flight by the young; (5) postfledging 2: from day 10 of the postfledging period onwards. The division of the postfledging period into two parts was associated with substantial differences in behavior of the young in the two periods, as recorded by personal observations at focal nests and by telemetry data on four young belonging to two broods: only after the first 10 days of the postfledging period the young showed efficient flying skills and good escape capabilities (Sergio et al. 2001). Whenever an individual hobby was sampled more than once during the same breeding stage, the average score for the stage was used for data analysis. Only one such average score was randomly selected for individuals sampled within more than one breeding stage, and employed in analyses requiring data independence.

Because the nest defense score was an ordinal variable, only nonparametric tests were carried out on that variable (Siegel and Castellan 1988). We used a general linear model with binomial errors and a logit link function (Crawley 1993) to test the effect of hobby breeding stage and mean intensity of nest defense on the proportion of dummy nests predated in each set placed near to the hobby after six days of exposure. In the case of covariation of two variables potentially influencing the intensity of defense, nonparametric Kendall's partial correlation analysis (Siegel and Castellan 1988) was employed to explore the effect of such variables on hobby defense behavior. When multiple tests were carried out on the same data set, significance probabilities were adjusted by the sequential Bonferroni correction (Rice 1989). All tests are two-tailed, statistical significance was set at $\alpha = 0.05$ and means are given with 1 SE.

TABLE 1. Presence of male and female Northern Hobbies at the nest site during nest defense trials (Po Plain, Northern Italy, 1992–1994).

Breeding stage	% Absence (n)[a]		P[b]
	Males	Females	
Incubation	12 (33)	0 (86)	0.013
Nestlings < 15 days old	20 (15)	0 (45)	0.005
Nestlings > 15 days old	33 (27)	9 (75)	0.010
Postfledging	36 (14)	2 (53)	0.001
Total	24 (89)	3 (259)	0.000[c]

[a] Percentage of visits in which the individual was recorded as absent.

[b] Difference in frequency of absence by males and females, tested by means of Fisher's exact test.

[c] Tested by means of χ^2 test.

Results. Although male presence declined progressively during the breeding cycle, females incubated eggs, brooded, and guarded nestlings during 97% of our nest visits (Table 1). Male absence was higher than that of females at all stages of breeding (Table 1).

Offspring mortality was expressed as percentage of eggs or chicks not surviving until the next breeding stage. Egg mortality was 17% ($n = 65$ eggs from 26 nests) and was higher than chick mortality ($\chi^2 = 5.34$, df = 1, $P = 0.042$). The actual difference may have been more pronounced, because most nest failures probably occurred early in incubation before our first nest check. Adding such 12 cases, and assuming that each of those pairs had laid at least one egg, raised the egg mortality rate from 17 to 30%. Nestling mortality was 3% during the first half of the nestling period ($n = 64$ chicks from 26 nests) and 0% during the second half ($n = 62$ chicks from 26 nests): the difference was not significant ($\chi^2 = 0.48$, df = 1, $P = 0.49$). Because the first checks during the nestling period were carried out when the nestlings were three to six days old, some early chick mortality may have gone unrecorded. Estimated offspring mortality thus probably decreases from incubation to fledging.

Within each stage of breeding, intensity of defense did not differ between females visited three times and more than three times during the breeding cycle (Table 2). Because in at least one study (Mallory and Weatherhead 1993) nest defense changed between the first and second visit, we compared intensity of defense between females visited only once (mean = 1.4 ± 0.1, $n = 13$) and more than once during incubation (mean = 1.7 ± 0.1, $n = 28$). The difference was not significant (U = 156.0, $z = -0.93$, $P > 0.05$). Finally, intensity of defense was not correlated with the previous number of visits by the researcher, when controlling for breeding stage (Kendall's rank partial correlation coefficient $T = -0.08$, $z = 0.76$, $n = 43$, $P > 0.05$). However, intensity of defense correlated positively with breeding stage when con-

TABLE 2.   Average (±1 SE) intensity of nest defense by female Northern Hobbies in relation to number of visits by the researcher (Po Plain, Northern Italy, 1992–1994).

Breeding stage	Number of visits by the researcher		Mann Whitney U (z)	P
	≤3 (n)[a]	>3 (n)[b]		
Incubation	1.6 ± 0.2 (20)	1.6 ± 0.1 (21)	207.5 (−0.07)	> 0.05
Nestling: first half	2.6 ± 0.3 (8)	2.7 ± 0.2 (19)	74.0 (−0.11)	> 0.05
Nestling: second half	3.5 ± 0.5 (10)	3.3 ± 0.4 (19)	81.5 (−0.63)	> 0.05
Postfledging	3.7 ± 0.6 (7)	3.8 ± 0.4 (16)	53.0 (−0.20)	> 0.05

[a] Based on nests visited ≤3 times during the whole breeding cycle, and with at least 15 days between successive visits.
[b] Based on nests visited >3 times during the whole breeding cycle.

trolling for previous number of visits (Kendall's partial correlation $T = 0.68$, $z = 6.40$, $n = 43$, $P < 0.0001$).

Intensity of defense during incubation did not vary significantly between males tested only once and more than once (Respectively, mean = 1.7 ± 0.1, $n = 23$; mean = 2.1 ± 0.4, $n = 9$; $U = 87.0$, $z = −0.80$, $P > 0.05$).

Intensity of defense did not correlate with previous number of visits when controlling for breeding phase (Kendall's partial correlation $T = −0.01$, $z = 0.12$, $n = 42$, $P > 0.05$), whereas defense intensity correlated positively with reproductive stage when controlling for previous number of visits (Kendall's partial correlation $T = 0.42$, $z = 3.92$, $n = 42$, $P = 0.0008$). Because there was no evidence for an effect of revisitation, further analyses were conducted pooling infrequently and frequently visited nests.

Female intensity of defense was higher than that of males during the 42 trials in which both partners

FIG. 1.   Average intensity of nest defense (±1 SE) by 42 male Northern Hobbies (open square) and 42 female Northern Hobbies (closed circle), simultaneously tested during 42 nest defense trials (Po Plain, Northern Italy, 1992–1994). Intensity of defense against a potential human predator was estimated through an ordinal aggressiveness score ranging from 1 (flies away and disappears) to 8 (stoops closely at the intruder).

were present at the same time (Wilcoxon matched pairs signed ranks test $z = −4.05$, $n = 42$, $P = 0.0008$; Fig. 1). Female intensity of defense was comparable to that of males during incubation (Wilcoxon matched pairs $z = −0.73$, $n = 15$, $P = 0.46$), and almost significantly higher during the other three stages (Wilcoxon matched pairs test; first half of nestling: $z = −2.37$, $n = 10$, $P = 0.063$; second half of nestling: $z = −2.37$, $n = 9$, $P = 0.063$; postfledging 1: $z = −2.20$, $n = 8$, $P = 0.055$; Fig. 1). There was a positive correlation between the defense intensity of both partners of each pair, even when controlling for breeding stage (Kendall's partial correlation $T = 0.44$, $z = 4.11$, $n = 42$, $P = 0.0001$).

Breeding stage. Intensity of defense increased during the breeding cycle, both for females with broods of two nestlings (Friedman repeated measures two-way ANOVA, $\chi^2 = 12.95$, $n = 11$, $P = 0.047$) and for females with broods of three nestlings (Friedman repeated measures two-way ANOVA, $\chi^2 = 20.01$, $n = 10$, $P = 0.0024$; Fig. 2).

Intensity of defense during incubation was not correlated with the number of eggs ($r_s = −0.21$, $n = 20$, $P > 0.05$), but tight-sitting females laid significantly more eggs than did loose-sitting females (respectively, 2.82 ± 0.4 and 2.30 ± 0.7, $t = −2.16$, $n = 11$, 10, $P = 0.04$), and fledged significantly more young (respectively, 2.56 ± 0.5 and 1.18 ± 1.2, $t = −3.33$, $n = 9$, 22, $P = 0.0001$). Intensity of nest defense was positively correlated with the number of fledged young when controlling for breeding stage (Kendall's partial correlation $T = 0.33$, $z = 3.15$, $n = 43$, $P = 0.016$; Fig. 2).

Past effort was measured as initial number of laid eggs following Wallin (1987) and Wiklund (1990). Clutch size was not correlated with intensity of defense during the second half of the fledging period, when controlling for brood size (Kendall's partial correlation $T = −0.11$, $z = 0.66$, $n = 19$, $P > 0.05$).

Defense intensity was not correlated with laying date when controlling for breeding stage (Kendall's partial correlation $T = 0.02$, $z = 0.13$, $n = 22$, $P > 0.05$).

Male intensity of defense increased during the breeding cycle (Kruskal Wallis one-way ANOVA, $\chi^2 = 7.40$, df = 3, $n = 42$, $P = 0.051$; Fig. 1).
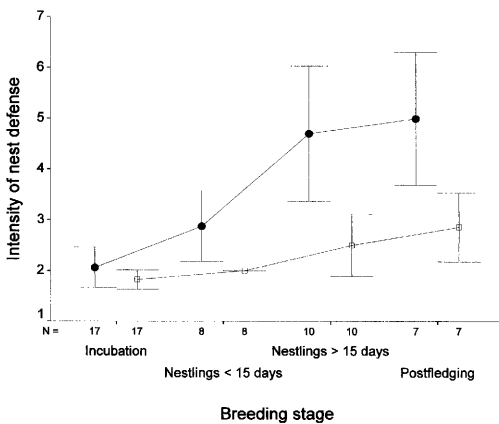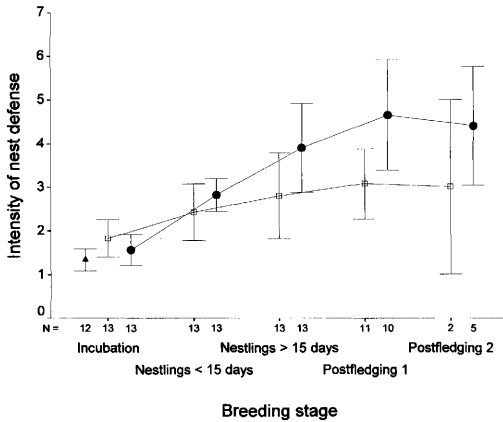
FIG. 2. Average intensity of nest defense (±1 SE) by hobby females who failed during incubation (triangle) and with broods composed by two (quadrat) and three (circle) nestlings. Data from 12 females that failed during incubation and 26 females visited at least once during incubation and the first and second half of the nestling period (Po Plain, Northern Italy, 1992–1994).

Defense intensity during incubation was not correlated with number of laid eggs ($r_s = -0.26$, $n = 7$, $P > 0.05$). There was no significant correlation between intensity of defense and number of fledged young when controlling for breeding stage (Kendall's partial correlation $T = -0.10$, $z = 0.90$, $n = 42$, $P > 0.05$).

Defense intensity was not correlated with laying date when controlling for reproductive phase (Kendall's partial correlation $T = 0.07$, $z = 0.46$, $n = 22$, $P > 0.05$).

Percentage of nests preyed upon by the sixth day of exposure was significantly higher for dummy control nests than for dummy nests near hobby nests (respectively, average percentage = 81 ± 5.2 and 46 ± 7.3, Wilcoxon matched pairs $z = -3.89$, $n = 36$, $P =$

0.0001). The minimal general linear model included mean intensity of nest defense, breeding stage, and interaction of those two variables as significant predictors of proportion of predated dummy nests within the sets placed near to the hobby (Table 3). When controlling for breeding stage, mean intensity of defense within each experiment was negatively correlated with percentage of predated dummy nests (Kendall's partial correlation $T = -0.40$, $z = 3.43$, $n = 36$, $P = 0.0006$). Distance of each dummy nest from the hobby nest entered a logistic regression model with survival or predation of 180 dummy nests near the hobby as the dependent variable ($B = -0.62$, Wald = 12.72, df = 1, $P = 0.0001$).

Discussion.—For both sexes, intensity of defense increased from incubation through fledging. The continued increase in defense during the first 10 days of the postfleging period, which is contrary to the predictions of Montgomerie and Weatherhead (1988) and Redondo (1989), may be in response to the limited escape capabilities of the young at that stage. The temporal increase in defense during the breeding cycle was not related to renesting potential because there was no correlation between defense intensity and laying date. In our population, fledging success was negatively related to laying date, as commonly reported for other avian species (review in Klomp 1970). The reproductive value of later broods was thus lower, selecting for lower levels of defense and dampening effect of any seasonal decrease in renesting potential, as also reported by Wallin (1987) and Wiklund (1990). We also doubt that increase of defense during the breeding cycle could be associated with the growing vulnerability or conspicuousness of the young, because raptor nestlings become darker, more cryptic, and increasingly capable of defending themselves as they age in the nest (O'Connor 1984, Wallin 1987). Cumulative past effort, expressed as initial number of eggs laid, was also not related to intensity of defense. Instead, the continuous increase in intensity of defense from one stage to the next, and even within the nestling period, closely mir-

TABLE 3. General linear model with binomial errors and a logit link function of predation of dummy nests ($n = 180$) positioned near Northern Hobby nests in the Po Plain, Northern Italy, between 1992 and 1994. The dependent variables is proportion of predated nests within each set of five dummy nests placed within 50 m of a Hobby nests ($n = 36$ sets of dummy nests). Predation was assessed every two days until, and including, the sixth day of exposure. Scaled deviance equaled 34.0 with 32 df and explained 73% of the overall deviance.

Variable	Parameter estimate	SE	t	df	P
Intensity of nest defense	−2.94	1.27	−2.32	32	<0.010
Breeding stage	−1.00	0.57	1.77	32	<0.050
Interaction between:					
Intensity of nest defense and breeding stage	0.66	0.34	1.94	32	<0.025
Constant	4.59	1.88	2.45	32	<0.010

rored the progressive increase in survival probabilities of the offspring. That is in agreement with predictions of parental investment theory, based on the growing reproductive value of the young, due to an increase in expected fitness benefits for the adults (Winkler 1987), or to the decreasing ratio between parent and young survival probabilities (Andersson et al. 1980).

As predicted by theoretical models of offspring protection (e.g. Redondo 1989), female intensity of defense was positively correlated with brood size at fledging. All else being similar (e.g. chick quality), large broods have greater reproductive value for the parent than smaller broods, and that may select for higher levels of optimal defense (Montgomerie and Weatherhead 1988). Positive correlations between level of defense and brood size have been reported in other studies (e.g. Knight and Temple 1986a, Wiklund 1990) and some authors have shown that parents respond rapidly to artificial manipulation of their broods, adjusting their defense responses to the current number of offspring potentially reaching independence (e.g. Knight and Temple 1986a, Wiklund 1990). Instead, there was no correlation between male intensity of nest defense and brood size.

Predation of dummy nests far from hobby nests was higher than at dummy nests near hobby nests. Furthermore, predation rates of dummy nests near falcons were positively related to distance from the hobby nest and negatively correlated with intensity of nest defense by the female hobby, when controlling for breeding stage. Thus, presence of the falcon probably lowered local predation pressure and more aggressive females deterred predation more than less aggressive ones: nest defense thus seemed to be beneficial and its intensity positively correlated with the derived benefit. As predators may not find nests until they are close to them, defense may be triggered when the predator crosses a certain threshold distance from the nest (Montgomerie and Weatherhead 1988) and, within that distance, intensity of defense increases as the predator approaches the nest (Andersson et al. 1980, Sproat and Ritchison 1993). If intensity of defense lowers nest predation and decreases with distance from the nest, dummy-nest predation rates would be expected to be positively related to distance from the hobby nest, as observed. In conclusion, hobby nest defense was a plastic trait, probably tuned to the reproductive value of the offspring. Parents apparently trade off costs and risks of the behavior with increasing likelihood of offspring survival.

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Do Golden-cheeked Warblers Select Nest Locations on the Basis of Patch Vegetation?

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ABSTRACT.—Proper management of endangered species requires an understanding of habitat use at a variety of spatial scales, and information on nesting habitat is especially important in that regard. We examined vegetation features associated with nest patches of the Golden-cheeked Warbler (*Dendroica chrysoparia*), a federally endangered migrant songbird that breeds only in central Texas. We used a spatially paired design to measure 13 vegetation variables at 43 nests and at an equal number of randomly chosen nonuse patches, one located near each nest. Canopy closure was greater at nest patches than at nonuse patches. However, none of the other vegetation variables differed between a nest patch and its paired nonuse patch on the same territory, despite high power to detect such differences. In contrast, 8 of the 13 variables exhibited significant variation among territories. For all 13 variables, effect size was substantially greater for variation between territories than for variation between nest patches and their paired nonuse patches. Lack of within-territory variation may reflect the scale at which vegetation varies in that habitat. Such a result suggests that territory selection may be more important than nest-patch selection in this species.

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Information on habitat use is critical for making proper management decisions (Verner et al. 1986). That is particularly true for endangered species, whose populations are often limited by availability of suitable habitat (Mayfield 1963, Scott et al. 1986, Jackson 1994). For birds, selection of nesting habitat is especially important, because nest location often affects reproductive success (Martin 1992, 1998) and, thus, population viability.

Defining "suitable habitat" requires a recognition that habitat selection is often hierarchical, especially when studying habitat used for a specific behavior such as nesting (e.g. Martin 1992, Steele 1993, Murphy et al. 1997). Nesting habitat can be quantified at a very broad scale (i.e. habitat features associated with presence or absence of a species), at the level of territory placement, at the level of nest patch within the territory, and, finally, as specific attributes of the nest site. Describing vegetation features associated with the nest patch is one of the key components of quantifying avian habitat requirements, particularly