The Condor 101:806–817

EURASIAN HOBBY DENSITY, NEST AREA OCCUPANCY, DIET, AND PRODUCTIVITY IN RELATION TO INTENSIVE AGRICULTURE[1]

FABRIZIO SERGIO[2] AND GIUSEPPE BOGLIANI
Dipartimento di Biologia Animale, University of Pavia, Piazza Botta 9, 27100 Pavia, Italy

Abstract. A Eurasian Hobby (*Falco subbuteo*) population of 13–18 breeding pairs was studied for 6 years from 1987 to 1995 in a 62 km^2 study area located within the seasonal flood zones of the Po River plain in northern Italy and characterized by intensive farmland interspersed with poplar (*Populus* sp.) plantations. Five percent of breeding attempts (n = 78 over the whole period) failed because of clear cutting of the nest tree and 4% because of human disturbance associated with clear cutting of the nesting woodlot. Fledging success was negatively related to laying date. Year after year, the nests of each pair were found in restricted traditional "nest areas," but not all nest areas were occupied every year, even if suitable woodlots were available within them. Occupation rate of nest areas was positively correlated with breeding success. The nestlings' avian diet was dominated by Swifts (*Apus apus*) and by *Passer* spp., accounting for 53 and 25%, respectively of 317 identified prey items. The local Eurasian Hobby population appeared to have adapted fairly well to the intensively managed agroforestry system, with recorded density and productivity in the range reported for other European populations in less intensively cultivated areas. We did not detect any decline in average density and productivity with increasing levels of agricultural change in various European populations. Possible reasons for this species' successful reproduction in modern agricultural landscapes include timing of breeding, tolerance of habitat fragmentation and of human activities near to the nest, tolerance of proximity to neighbors, type of diet, and absence of important predators.

Key words: adaptation to intensive farmland, diet, Eurasian Hobby, Falco subbuteo, *nest area occupation rate, nest dispersion, productivity.*

INTRODUCTION

The Eurasian Hobby (*Falco subbuteo*) is a small sized falcon found in open lowland, generally nesting in unused crow (*Corvus corone*) nests in tall trees (Bijlsma 1997). All over Europe, the Eurasian Hobby is relatively common in cultivated landscapes (Fuller et al. 1985, Bijlsma 1993, Bogliani et al. 1994). However, few studies have been carried out in areas of intensive farmland (Fuller et al. 1985, Parr 1985). Local population increases and declines have been reported (Bijlsma 1997). On the whole, the Eurasian Hobby is one of the least studied European raptors, probably due to its low detectability during the breeding season and consequent difficulties in finding nests (Bogliani 1992, Parr 1994). There are still no explanations for its adaptation to modern agricultural landscapes. In this paper we report the results of a 6-year study on a Eurasian Hobby population in an intensively managed agroforestry system in northern Italy.

This paper focuses on (1) a quantitative description of the breeding ecology of the local Eurasian Hobby population, (2) a comparison of density and productivity estimates of the local population with those of other European populations in similar, or more "natural" environments, and (3) aspects of their breeding ecology which have allowed the Eurasian Hobbies to colonize areas of extremely intensive farmland.

METHODS

STUDY AREA

The study area extended along a 40 km stretch of the Po River in northern Italy, between the confluence with the Tanaro River and with the Ticino (45°N, 9°E), and comprised 62 km^2 of the seasonal flood plain of the Po River. Altitude ranged from 54 to 80 m above sea level. Over 30% of the area was covered by poplar (*Populus* × cultivar) plantations. Within plantations, poplars are planted with a regular spacing, in a quadrat or rectangular design with a distance of

[1] Received 20 July 1998. Accepted 8 April 1999.
[2] Current address: Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, OX1 3PS, Oxford, U.K., e-mail: fabrizio.sergio@zoo.ox.ac.uk

5–6 m between trees and a usual density of 320–350 trees ha^{-1}. Poplars grow very rapidly: most plantations are felled during their 10th–12th year of age. By this time trees are on average 22–23 m high with a diameter at breast height (dbh) of 30–32 cm (Prevosto 1965).

Mature woodland dominated by pedunculated oak (*Quercus robur*) was the primary habitat occupying the more fertile soils in historical times, but this has been completely replaced by cultivation. The few woodlots other than poplar plantations mainly consisted of small clumps of artificially introduced young locust trees (*Robinia pseudacacia*) along slight escarpments, and white willow (*Salix alba*) woodlots bordering rivers or irrigation ditches.

The remaining two thirds of the study area were dominated by intensive agriculture; maize and soybean were the most common crops. Uncultivated areas were scarce (< 6%) and mainly consisted of fallow fields, reedbeds, and the Po River sand and shingle banks and islets, which were covered by herbaceous vegetation and by willow (*Salix* spp.) bushes and trees. Human presence in the study area was low during the summer and was mainly associated with agricultural activities.

DATA COLLECTION

The local Eurasian Hobby breeding population was systematically censused in 1987 and 1988, and from 1992 to 1995. Because of the low detection rate of pairs which did not lay eggs, only data on the breeding sector of the population were included in the analyses.

To minimize the risk of nest desertion early in incubation (Grier and Fyfe 1987), we started looking for hobby nests during the last week of June, one week after the local average egg laying date (19 June, n = 56). Hobby nests were censused by checking all the Hooded Crow (*Corvus corone cornix*) nests on trees at least 7 m high. When no hobby nests were found in this way, searches were carried out on smaller trees. Census activities were aided by the presence of Common Woodpigeons (*Columba palumbus*), frequently breeding near Eurasian Hobby nests in our study area (Bogliani et al. 1999).

Nest site dispersion was analyzed by means of the G-statistic (Brown 1975), calculated as the ratio between the geometric mean and the arithmetic mean of the squared nearest neighbor distances (NNDs). The index ranges from 0 to 1; values close to 1 (> 0.65) indicate a uniform distribution of nests (Brown 1975).

To collect data on productivity, each nest was visited at least three times, the first during incubation, the second just after hatching, and the third when the young were ready to fledge (> 25 days old). Nest contents were checked by directly climbing the nest tree or by means of a mirror attached to the end of a telescopic steel pole. Laying date was calculated by subtracting 30 days from the date of hatching. Hatching date was calculated by backdating nestlings from feather development, using personal observations at focal nests and information contained in Morata (1971), Mayer-Gross (1972), and Cramp and Simmons (1980). Older nestlings were more difficult to backdate and we discarded from analyses data based on backdating of nestlings older than 10 days of age.

Fledging dates were recorded for 39 chicks belonging to 15 broods by visiting each nest daily, once the oldest nestling was 25 days old, following the procedure reported by Viñuela and Bustamante (1992). Fledging age was calculated as the number of days between fledging date and hatching date, which was estimated by backdating nestlings less than 6 days old (first down) when first inspected.

Between 1992 and 1995, Eurasian Hobby avian prey remains were collected during each nest visit by thoroughly inspecting the ground in the nesting woodlot. Very few remains were found in 1995 (n = 25) and they were not included in analyses of diet variation in relation to year or breeding phase. We presume these prey were given to the chicks, as adults usually pluck and feed on their own far from the nest (Cramp and Simmons 1980).

Following the terminology proposed by Steenhof (1987), a breeding pair was one which laid eggs, a successful pair was one which reared at least one young to fledging age, and productivity was expressed as nesting success (percentage of nests which fledged at least one chick), and mean number of young fledged per breeding pair and per successful pair. The term "nest area" is used to denote an area where more than one nest was found in different years, but where only one Eurasian Hobby pair nested within any one year (Fuller et al. 1985, Parr 1985). Despite the high variability in nearest neighbor distances (NND), nest areas of different pairs were always clearly separated from each other. Contemporaneous occupation of neighboring nest areas by different pairs clarified any dubious cases. To identify the factors potentially affecting nest area occupation rates, we first calculated the arithmetic center of each nest area. We then recorded the distance of the nest area center from the nearest wetland, village, and dirt road, the minimum number of suitable woodlots present each year within 800 m of the nest area center, and the length of roads within 800 m of the nest area center. A suitable woodlot was defined as any mature (dbh > 25 cm) poplar plantation or willow woodlot more than 200 m from the nearest dirt road (Sergio and Bogliani 1995).

STATISTICAL ANALYSES

When data were not normally distributed, they were $\log_e$ transformed, square-root transformed, or arcsine square-root transformed as necessary (Sokal and Rohlf 1981). When transformed data still did not approach normality, nonparametric tests were employed (Siegel and Castellan 1988). When multiple comparisons were carried out on a set of values, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989). All tests are two-tailed and statistical significance was set at $\alpha = 0.05$. Values presented are means ± SE.

RESULTS

DENSITY

The number of breeding pairs in the 62 km^2 study area ranged from 12 to 18 (Table 1), giving a density ranging from 19.3 pairs $100\text{-}km^{-2}$ in 1988 to 29 pairs in 1987; the overall mean density was 23.9 breeding pairs $100\text{-}km^{-2}$ (Table 1).

NEST SITES

Only Hooded Crow nests were selected by the Eurasian Hobby. Such nests had always been built by crows the preceding spring. Of 115 Eurasian Hobby nests located between 1985 and 1995, 110 were within commercial poplar plantations; the remaining 5 were in willow woodlots. Tree species was determined for 299 crow nest trees located within 800 m of 25 Eurasian Hobby nests; there was no significant selection of poplars by the Eurasian Hobby (Fisher exact test, $P = 0.24$), whose choices thus reflected those of Hooded Crows. Mean Eurasian Hobby nest tree dbh was 33 ± 1 cm ($n = 27$); average nest tree height was 23 ± 1 m ($n = 27$); mean nest height was 15.4 ± 0.6 m ($n = 27$). Nesting woodlot size ranged from 0.5 ha to 33.3 ha, averaging 7.6 ± 1.7 ha ($n = 27$). No Eurasian Hobby nests were found on single lines of trees or on isolated trees, although crow nests were often available in such situations.

NEST SITE DISPERSION

Mean NND, logarithmically transformed, did not vary among years (ANOVA, $F_{5,82} = 2.2$, $P = 0.06$) and ranged from 1,345 m in 1988 to 2,102 m in 1992 (Table 1). Overall average NND was 1,798 m ($n = 89$). Eighty-two percent of the pairs had NNDs of 500–2,500 m. Values of the G-statistic showed a uniform dispersion of nest sites in 1987, 1993, 1994, and 1995, but nonuniform dispersion in 1988 and 1992 (Table 1). Pooling data from all years, the overall G-value was 0.69, indicating a uniform distribution of nests.

PHENOLOGY

Median egg laying date was significantly later in 1995 than in the other years ($F_{5,52} = 3.56$, $P = 0.008$, Duncan's multiple range test, $P < 0.05$, Table 1). Pooling data from all years, mean egg laying date was 19 June ± 1 day (min. 9 June, max. 10 July, $n = 56$). Eighty-two percent of the clutches ($n = 56$) were laid between 10 and 25 June. Egg laying dates of two repeat clutches, not included in the above analyses, were 7 and 10 July.

Eurasian Hobbies usually start incubating after laying the second egg; the third egg is usually laid two days after the second (Cramp and Simmons 1980, Fiuczynski and Nethersole-Thompson 1980). Although hatching dates were estimated by backdating nestlings (< 6 days old) and thus could have wide latitude, the dates for the 14 broods for which we recorded both fledging and hatching dates seemed to reflect this rule accurately. Fledging asynchrony did not differ from hatching asynchrony (Wilcoxon sign rank test, $z = -1.35$, $n = 14$, $P = 0.18$). All young ($n = 37$) fledged between 8 August and 5 September. Fledging date for two young from a replacement clutch was 15 September. The period of nest-dependency did not vary among years ($F_{3,33} = 1.1$, $P = 0.34$), or with fledging order ($F_{2,34} = 0.9$, $P = 0.41$). Pooling years and nestlings of different fledging order, mean fledging

TABLE 1. Density, nearest neighbor distances (m), *G*-statistic, laying date, and productivity estimates for the local Eurasian Hobby population in the 6 years of study (1987–1995).

Year	Number of censused nests	Density (breeding pairs 100-km^{-2})	Nearest neighbor distance (m): x ± SE (range)	*G*-statistic	Laying date: x ± SE (range)[a]	Nests checked for productivity	Mean clutch size[b]	Successful nests (%)	Mean number of fledged young	
									Per breeding pair	Per successful pair
1987	18	29	1,663 ± 133 (700–2,575)	0.78*	18.3 ± 2.0 (9–40)	13	2.88 ± 0.26	12 (92)	2.07 ± 0.26	2.25 ± 0.21
1988	12	19.3	1,346 ± 301 (200–3,350)	0.45	18.4 ± 1.4 (14–26)	7	2.50 ± 0.33	7 (100)	2.29 ± 0.18	2.29 ± 0.18
1992	16	25.8	2,103 ± 338 (730–4,320)	0.58	18.2 ± 1.3 (12–27)	16	2.40 ± 0.24	12 (75)	1.81 ± 0.33	2.42 ± 0.19
1993	16	25.8	2,095 ± 239 (930–2,340)	0.70*	13.3 ± 0.1 (9–19)	16	2.73 ± 0.20	11 (69)	1.81 ± 0.33	2.64 ± 0.15
1994	14	22.6	1,636 ± 134 (850–2,340)	0.86*	17.2 ± 0.1 (15–20)	14	2.57 ± 0.20	9 (64)	1.43 ± 0.32	2.22 ± 0.22
1995	13	21	1,802 ± 194 (1,140–3,100)	0.75*	29.9 ± 3.2 (21–45)	12	—	7 (58)	1.33 ± 0.36	2.29 ± 0.18
total	89	23.9[c]	1,798 ± 97 (200–4,320)	0.69*	18.8 ± 0.1 (9–45)	78	2.65 ± 0.11	58 (74)	1.76 ± 0.13	2.36 ± 0.08

[a] Sample size for laying date is 16 nests in 1987, 8 in 1988, 11 in 1992, 9 in 1993, 5 in 1994, 7 in 1995, and 56 overall.
[b] Sample size for mean clutch size is 9 nests in 1987, 8 in 1988, 5 in 1992, 11 in 1993, and 7 in 1994. Data for 1995 not given because based on only 2 nests.
[c] Mean density across years.
* $G > 0.65$, indicating a uniform distribution of breeding sties.

TABLE 2. Causes of breeding failure of the Eurasian Hobby population in the Po Plain in the 6 years of study (1987–1995).

Cause of breeding failure	Number (%) Incubation	Fledging
Clearcutting of the nest	—	4 (17)
Human disturbance connected with clearcutting activities	3 (13)	—
Human disturbance by shepherds with sheep flock	1 (4)	—
Unknown	16 (67)	—
Total	20 (83)	4 (17)

age was 31.2 ± 0.5 days (n = 37 nestlings from 14 broods).

BREEDING SUCCESS

No significant differences among years were detected for mean clutch size ($F_{4,35} = 0.5$, $P = 0.71$), mean number of young fledged per breeding pair ($F_{5,72} = 1.0$, $P = 0.40$), or mean number of young fledged per successful pair ($F_{5,52} = 0.6$, $P = 0.66$). Data from different years were thus pooled (Table 1). Productivity estimates are outlined in Table 1. Only 3 out of 42 clutches checked in 6 years of research were composed of 4 eggs.

FACTORS AFFECTING BREEDING SUCCESS

Twenty out of 24 nest failures (83%) occurred during incubation (Table 2). The other four occurred during the fledging period. Causes of nest failure included clearcutting and human disturbance. In the other 16 cases, the cause of failure was unknown; in 2 of these 16 cases the clutch was abandoned for no clear reason by the resident pair and progressively preyed upon by Hooded Crows. Disturbance caused by clearcutting of the nesting woodlot or of nearby areas is hence the likely explanation for the failure of 9% of all breeding attempts (n = 78).

Eurasian Hobbies never used the same crow nest in consecutive breeding seasons, when the nest was still present and apparently in good condition. They tended to return to the same nesting woodlot as the preceding year (40.6%, n = 32), as long as it had not been felled in the intervening winter. However, in many cases they spontaneously changed nesting woodlot (31.3%, n = 32), or were forced to do so because of the felling of the old plantation (28.1%, n = 32). Even when changing nesting woodlot, each Eurasian Hobby pair always tended to select a crow nest within a traditional nest area. Distances between old and new sites within the same nest area in consecutive breeding seasons ranged from 30 m to 1,700 m, averaging 446 ± 75 m (n = 28). Year after year, the nest of each pair was located within its traditional nest area, but not all nest areas were occupied by breeding falcons every year. Although some nest areas were always occupied whenever there were suitable woodlots within them, others were rarely occupied. In particular, the percentage of years that a nest area was occupied was significantly positively correlated with mean clutch size for that territory ($r_s = 0.58$, $n = 15$, $P = 0.05$), hatching success ($r_s = 0.65$, $n = 19$, $P = 0.01$), mean number of fledged young ($r_s = 0.83$, $n = 21$, $P = 0.001$), with breeding success ($r_s = 0.88$, $n = 21$, $P = 0.001$), and negatively correlated with the percentage of breeding attempts failed during incubation ($r_s = -0.88$, $n = 21$, $P = 0.001$, Table 3). The correlation between level of occupation and mean laying date was not significant ($r_s = -0.33$, $n = 17$, $P = 0.19$, Table 3).

Nest areas which were always occupied had a significantly lower amount of roads within 800

TABLE 3. Productivity of the local Eurasian Hobby population in relation to the occupation rate of the nest area (1992–1995).

Occupation rate[a]	Nests (territories)	Laying date (x ± SE)[b]	Clutch size (x ± SE)[c]	% eggs hatched[d]	Fledged young (x ± SE)	% successful nests	% nests failed in incubation
0–25%	3 (3)	—	—	0	0 ± 0	0	100
25–50%	5 (3)	19.5 ± 0.5	2	66	0.80 ± 0.49	40	60
50–75%	7 (3)	18.5 ± 3.5	2.60 ± 0.50	69	1.57 ± 0.57	57	43
75–100%	37 (12)	16.9 ± 1.4	2.80 ± 0.10	83	2.00 ± 0.17	82	14

[a] Percentage of years in which the territory was occupied.
[b] Sample sizes for each class of occupation were 0, 2, 2, 20, respectively.
[c] Sample sizes were 0, 1, 5, 15, respectively.
[d] Sample sizes were 3, 3, 6, 17, respectively.

TABLE 4. Avian prey of Eurasian Hobby nestlings, based on a sample of 317 items identified at the species or genus level and collected in the period 1992–1995. Taxonomic groups accounting for less than 1% of the total prey items are not shown and are included in the category "Other birds." Frequency of main prey categories in relation to breeding stage also is shown.

Prey species	Number (%)	Weight[a] (%)	Frequency of main prey categories[b] (%)		
			Incubation (n = 17)	Fledging (n = 228)	Postfledging (n = 47)
Common Swift *Apus apus*	169 (53.3)	7,267 (46)	7 (41)	125 (55)	31 (66)
Passer spp.	80 (25.2)	1,977.5 (12.5)	6 (35)	61 (27)	7 (15)
Unidentified	53 (16.7)	1,298.5 (8.2)			
House Sparrow *P. domesticus*	17 (5.4)	459 (2.9)			
Eurasian Tree Sparrow *P. montanus*	10 (3.2)	220 (1.4)			
Others	68 (21.5)	6,570 (41.5)	4 (24)	42 (18)	9 (19)
Barn Swallow *Hirundo rustica*	19 (6)	389.5 (2.5)			
House Martin *Delichon urbica*	7 (2.2)	126 (0.8)			
Common Wood Pigeon *Columba palumbus*	5 (1.6)	2,425 (15.3)			
Rock Pigeon *Columba livia*	5 (1.6)	1,350 (8.5)			
Sky Lark *Alauda arvensis*	5 (1.6)	197.5 (1.2)			
Great Tit *Parus major*	4 (1.3)	740 (4.7)			
Columba spp.	4 (1.3)				
Other birds[a]	19 (6)	1,342 (8.5)			
Unidentified birds	28				

[a] Fresh weight, measured in g.
[b] Main prey categories are: swifts, *Passer* spp., and Others.
[c] Category "Other birds" include: Great Spotted Woodpecker *Dendrocopos major* (2), Common Starling *Sturnus vulgaris* (3), Eurasian Jay *Garrulus glandarius* (1), European Greenfinch *Carduelis chloris* (1), White Wagtail *Motacilla alba* (1), Grey Wagtail *M. cinerea* (1), Yellow Wagtail *M. flava* (1), Chaffinch *Fringilla coelebs* (1), European Bee-eater *Merops apiaster* (2), Common Tern *Sterna hirundo* (1), Little Owl *Athene noctua* (1).

m of the center than nest areas which were not occupied every year (t_{19} = 2.42, P < 0.05). In contrast, no such difference was detected in minimum yearly availability of suitable woodlots and in distance from the nearest dirt road, village, wetland, or neighboring nest area (all t_{19} < 1.44). The nest area occupation rate was still positively correlated with mean fledging success even when controlling, through partial correlation analysis, for amount of roads within 800 of the nest area center (r = 0.84, n = 21, P = 0.001).

AVIAN PREY OF THE NESTLINGS

The nestlings' diet was mainly composed of two types of prey: swifts and sparrows (Table 4). Swifts and *Passer* spp. made up 49% and 27%, respectively of the prey in 1992 (n = 41), 61% and 21%, respectively in 1993 (n = 176), and 47% and 36%, respectively in 1994 (n = 75). As the association between year and frequency of prey categories in the diet was not significant (χ^2_4 = 8.03, P = 0.18), data from different years were pooled. On the whole, swifts and sparrows constituted 53% and 25%, respectively of 317 prey items, identified between 1992 and 1995 (Table 4). Thus, 79% of the prey belonged to only three species. Of the 169 swifts captured, 19% were juveniles.

Similar findings were revealed by the analysis of prey biomass (Table 4): diet was dominated by swifts, Common Woodpigeons, sparrows, and Rock Pigeons. Actually, the last two species featured only because of their weight, and were rarely preyed upon by the hobby (1.6 % of prey items by number). Eighty-nine percent of prey items had a body weight of 20–50 g. Frequency of main prey categories did not change through the breeding season (χ^2_4 = 4.6, P = 0.33, Table 4).

ADAPTATION TO INTENSIVE FARMLAND

To investigate whether breeding in intensive farmland habitats limited the rate of reproduction, we compared our estimates of density and productivity with those of other European populations in less intensively cultivated areas. The habitat of each study area was classified according to the following ordinal score: (1) semi-natural habitats, with less than 30% of the area under cultivation, (2) farmland, with 30–70% of the area under cultivation, and (3) intensive farmland, with more than 70% of the area under cultivation.

Published estimates of density, nest spacing, clutch size, nesting success, and number of fledged young are shown in Table 5 and 6. Estimates from our study area were in the range of those reported elsewhere despite human intervention in the habitat, and density and mean nearest neighbor distance were the highest and the lowest ever recorded. In particular, clutch size was significantly larger in England and in the Wadden Sea islands (Fiuczynski and Nethersole-Thompson 1980, Bijlsma and Van Diermen 1986) than in our study site ($F_{6,666} = 6.4$, $P = 0.001$, Duncan's multiple range test, $P < 0.05$, Table 6). Mean number of fledged young per breeding pair was significantly higher in our study area and in Berlin than in the north of Berlin ($F_{2,498} = 6.0$, $P = 0.003$, Duncan's multiple range test, $P < 0.05$, Table 6). Mean number of fledged young per successful pair did not vary among populations ($F_{6,534} = 1.1$, $P = 0.38$, Table 6). The frequency of successful breeding attempts in our study site was not significantly different from that recorded in the English New Forest, chalk downland and river valley (3 comparisons, χ^2 tests, all $P > 0.05$), from that in Berlin ($\chi^2_1 = 2.8$, $P > 0.05$), or from that in the north of Berlin ($\chi^2_1 = 3.8$, $P > 0.05$, Table 6). Finally, mean nearest neighbor distance in our study area was lower than that in the English New Forest, chalk downland and river valley (3 comparisons, $t_{96-101} > 6.3$, $P < 0.01$, Table 5). No significant correlation was detected between the habitat change ordinal score and density, mean NND, mean clutch size, percentage successful nests, and mean number of fledged young per breeding pair, or per successful pair ($r_s < 0.41$, $n = 6$–12, $P > 0.05$).

DISCUSSION

BREEDING ECOLOGY OF THE LOCAL POPULATION

In our study area, Eurasian Hobbies were highly dependent on managed poplar plantations and Hooded Crows for nesting. As in other studies (Parr 1985, Bijlsma 1993), Eurasian Hobbies nested on tall, mature trees. Poplar plantations started to be suitable for Eurasian Hobbies when they were about 8 years old, but, because of their fast growth rates, they were clear cut at about 12 years of age. Thus Eurasian Hobbies continually had to shift from one plantation to another, as old nesting woodlots were felled and new ones in the surroundings grew older. Notwithstanding such a dynamic environment, nests were usually found in restricted traditional nest areas year after year, as also reported by others for this species (Fuller et al. 1985, Parr 1985) and as is typical of other raptors (Newton 1991). The use of traditional nest areas by raptors is probably caused by the inherent superiority of certain areas over local alternatives and by the need for incoming birds to fit within the existing territorial framework (Newton 1979). Still, not all nest areas were occupied every year. Some were rarely occupied even when suitable plantations were available. Such nest areas had a higher extent of roads within 800 m of their center than nest areas which were always occupied. In our study site, Eurasian Hobbies were shown to select crow nests farther away from the nearest road than available, and proximity to such sources of human disturbance negatively affected productivity (Sergio and Bogliani 1995). Finally, independently from the amount of roads in the nest area surroundings, the occupation rate of nest areas was positively correlated with breeding performance within them. This suggests that other factors also are involved in determining the quality of nest areas. Food availability, that we were unable to measure, was probably one of them. The connection between occupation rate and productivity could also be due to the interaction between habitat quality and bird quality, the best individuals occupying the best nest areas and vice versa, as shown by Matthysen (1990) and Newton (1991).

In summary, nest areas varied in quality in relation to their degree of potential human disturbance and, probably, food availability. Eurasian Hobbies recognized such variations and responded by settling in high quality areas, where they attained a higher productivity, more often than in low quality ones. Such a pattern of settlement is in agreement with the ideal despotic model of bird distribution proposed by Fretwell and Lucas (1970). In this model, the best competitors, or the first individuals to arrive, occupy the highest quality nest areas, thus preempting their occupancy by other individuals through territorial behavior (Pulliam and Danielson 1991). Lower quality or later arriving individuals settle on progressively lower quality nest areas. Heterogeneity in nest area occupation and breeding output also can be of great value for applied

TABLE 5. Density and nearest neighbor distances (NND) of some Eurasian Hobby populations in Europe.

Study area location (period)	Habitat	*n*	Density[a]	Mean NND (km)	Source
England					
New Forest (1982)	Healthland	14	4.9	3.9	Parr 1985
Chalk downland (1982)	Farmland	9	1.6	5.0	Parr 1985
River valley (1982)	Farmland	7	2.8	4.0	Parr 1985
Southern midlands A (1975–1983)	Arable farmland	6	3.8	4.4	Fuller et al. 1985
Southern midlands B (1975–1983)	Mixed farmland	7	4.8	4.8	Fuller et al. 1985
Cambridgeshire	Arable farmland	14	13	8.8	Prince and Clark 1993
Germany					
Middle Elbe (1981)	Riverine forest	—	1.4	—	Steinke 1987
Kreis Zerbst (1981)	Arable farmland	—	2.8	—	Steinke 1987
Fläming (1981)	Pine forest	—	2.1	—	Steinke 1987
Postdam (1987–1990)	Boggy lowland	38	1–3.18	—	Hastädt and Fielder 1991
Rumania					
Danube delta	Wetland	300	6.9	—	Müller and Rohde 1991
Italy					
Po Plain (1987–1995)	Intensive farmland and poplar plantations	89	23.9	1.8	This study

[a] Number of nests, pairs, or territories $100 \cdot km^{-2}$.

TABLE 6. Productivity of some Eurasian Hobby populations in Europe.

Study area location (period)	Habitat	No. nests	Mean clutch size (*n*)	% successful nests	Mean number of fledged young per Breeding pair	Mean number of fledged young per Successful pair	Source
England							
New Forest	Healthland	25	—	92	1.88	2.04	Parr 1985
Chalk downland	Farmland	16	—	93.8	2.00	2.13	Parr 1985
River valley	Farmland	10	—	80	1.70	2.13	Parr 1985
Wiltshire, Surrey, Berkshire (1930–1976)	Farmland	114[a]	2.9 (236)	—	—	2.02	Fiuczynski and Nethersole-Thompson 1980
Germany							
North of Berlin (1941–1944)	Farmland	32	—	53.1	1.09	2.06	Wendland 1953
Berlin (1956–1978)	Urban	391	2.7 (269)	77.5	1.86	2.41	Fiuczynski and Nethersole-Thompson 1980
Berlin (1977–1988)	Urban	143	—	62.2	—	2.4	Fiuczynski 1991
Zerbst (1981–1985)	Arable farmland	11	3.3 (12)	—	2.4	3.00	Steinke 1987
Postdam (1987–1990)	Boggy lowland	38	2.52 (24)	42	—	2.1	Hastädt and Fielder 1991
Netherlands							
Veluwe (1972–1979)	Farmland	126[a]	2.8 (64)	—	—	2.3	Bijlsma 1980
Wadden Sea Islands (1966–1985)	—	28[a]	3.1 (27)	—	—	2.6	Bijlsma and van Diermen 1986
Northern Netherlands (1984–1991)	Farmland	49[a]	3.0 (21)	—	—	2.3	Bijlsma 1994
Rumania							
Danube Delta (1981–1988)	Farmland	48[a]	—	—	—	2.44	Müller and Rohde 1991
Italy							
Po Plain (1987–1995)	Intensive farmland, poplar plantations	78	2.7 (40)	74	1.76	2.36	This study

[a] Only successful pairs censused.

conservation purposes. Efforts should be directed at identifying high quality nest areas and protecting them, thus increasing the cost-effectiveness of conservation. For example, between 1992 and 1995, nest areas which were always occupied made up 57% of the total sample (n = 21), but contributed to 83% of all chicks fledged by the population.

The use of traditional nest areas probably favored the uniform dispersion of nest sites, but Eurasian Hobbies also showed a remarkable flexibility in NNDs, which ranged from a minimum of 200 m to a maximum of 4,320 m. Such high variation in NNDs has been recorded in other areas too (Fiuczynski and Nethersole-Thompson 1980, Fuller et al. 1985, Parr 1985).

ADAPTATION TO INTENSIVE FARMLAND

Many raptors and other birds are negatively affected by the environmental changes brought about by agricultural activities (Olendorff 1993, Pain and Pienkowski 1997). In contrast, our Eurasian Hobby population seemed to be compatible with the current agricultural practices. The probability of successfully raising chicks was positively related to the proportion of cultivated open areas within 800 m of the nest (Sergio and Bogliani 1995). Observed density and productivity were comparable or even higher than those of other European populations in more natural environments, and the degree of habitat alteration did not significantly affect average estimates of density and productivity across Europe. In Great Britain, Eurasian Hobby populations have recently increased (Parr 1994), despite the progressive agricultural intensification negatively affecting many farmland bird species (Pain and Pienkowski 1997).

We suggest that various aspects of this falcon life history allow it to breed successfully in areas of intensive agriculture. Late breeding allows them to nest in periods of low human activity in cultivated fields. The period of residence in breeding quarters (mid April–October) shows almost no overlap with local hunting seasons, thus minimizing the danger of illegal shooting. Mechanization of agricultural practices decreases time spent by farmers near breeding sites, lowering the impact of disturbance. In Italy, some Eurasian Hobby pairs seemed to be extremely tolerant of human beings inside tractors, some Eurasian Hobbies even continued incubation while the ground just under the nest was being ploughed. The ability to nest in small woodlots, lines of trees, and even single trees increases the availability of potential breeding sites in a manner compatible with the high degree of habitat fragmentation typical of current agricultural landscapes. Such fragmentation also increases the amount of open areas, suitable for this falcon's hunting habits. High densities of breeding crows, often associated with farmland habitats, determine the presence of a rich supply of potential breeding sites; good availability of potential nests is the prerequisite for the falcon's ability to select the best one among them, for example the farthest from potential sources of human disturbance. Flexibility of inter-nest spacing patterns favors more efficient use of unpredictably available crow nests and mature woodlots, especially when the latter are managed for commercial purposes. The adult and nestling diet is usually dominated by flying insects (Glutz et al. 1971, Parr 1985), and birds of the families Apodidae, Hirundinidae, Passeridae, and Alaudidae, which are generally abundant in cultivated landscapes. There are few competitors for such prey, especially for swifts, swallows, and martins. Finally, top predators such as Goshawks (*Accipiter gentilis*), or Eagle Owls (*Bubo bubo*), potentially capable of depressing the falcon survival rate, breeding density and productivity (Fiuczynski 1991, Mikkola 1983), are generally absent or rare in intensive farmland.

However, breeding in farmland also involved some drawbacks, such as increased levels of human disturbance, potential egg predation by crows, nest failures caused by tree felling operations, and non-laying caused by absence of suitable woodlots. Problems connected with organochlorine compounds have been observed recently in Germany (Bijlsma 1997). Basic environmental ameliorations aimed at Eurasian Hobby conservation would include reducing the pesticide output, increasing the regular availability of mature woodlots, and expanding insect rich habitat types, such as wetlands or fallows.

ACKNOWLEDGMENTS

We thank L. Marchesi for identifying collected prey remains, and G. Tavecchia and E. Tiso for help in the field. B. Arroyo, S. J. Parr, G. Tavecchia, and an anonymous reviewer provided constructive comments on an earlier version of the manuscript. Partial funding was provided in 1992 and 1993 by Regione Lombardia, Servizio Faunistico. F.S. was awarded the grant

"Edoardo Bianchi" by the University of Pavia in 1993.

LITERATURE CITED

BIJLSMA, R. G. 1980. De Boomvalk. Kosmos, Utrecht, Netherlands.

BIJLSMA, R. G. 1993. Ecologische atlas van de Nederlandse roofvogels. Schuyt, Haarlem, Netherlands.

BIJLSMA, R. G. 1997. Hobby, p. 186–187. *In* W. J. M. Hagemeijer and M. J. Blair [EDS.], The EBCC atlas of European breeding birds, their distribution and abundance. T and AD Poyser, London.

BIJLSMA, R. G., AND J. VAN DIERMEN. 1986. De Boomvalk *Falco subbuteo* als broedvogel op de Nederlandse Waddeneilanden. Limosa 59:135–137.

BOGLIANI, G. 1992. Lodolaio (*Falco subbuteo*), p. 651–658. *In* P. Brichetti, P. De Franceschi, and N. Baccetti [EDS.], Fauna d'Italia—Aves. Vol. 1. Calderini Edicion, Bologna, Italy.

BOGLIANI, G., F. BARBIERI, AND E. TISO. 1994. Nest-site selection by the Hobby (*Falco subbuteo*) in poplar plantations in northern Italy. J. Raptor Res. 28:13–18.

BOGLIANI, G., F. SERGIO, AND G. TAVECCHIA. 1999. Woodpigeons nesting in association with hobby falcons: advantages and choice rules. Anim. Behav. 57:125–131.

BROWN, D. 1975. A test of randomness of nest spacing. Wildfowl 26:102–103.

CRAMP, S., AND K. E. L. SIMMONS. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2. Hawks to bustards. Oxford Univ. Press, Oxford.

FIUCZYNSKI, D., AND D. NETHERSOLE-THOMPSON. 1980. Hobby studies in England and Germany. British Birds 73:275–295.

FIUCZYNSKI, D. 1991. Feinddruck und nistplatz-angebot als limitierende faktoren für siedlungsdichte und bruterfolg beim Baumfalken (*Falco subbuteo*), p. 63–71. *In* R. D. Chancellor and B. U. Meyburg [EDS.], Birds of prey Bulletin No. 4. Lentz Druck, Berlin.

FRETWELL, S. D., AND J. H. J. LUCAS. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16–36.

FULLER, R. J., J. K. BAKER, R. A. MORGAN, R. SCROGGS, AND M. WRIGHT. 1985. Breeding populations of the Hobby *Falco subbuteo* on farmland in the southern Midlands of England. Ibis 127: 510–516.

GLUTZ, U. N., K. M. BAUER, AND E. BEZZEL. 1971. Handbuch der Vögel Mitteleuropas. Vol. 4. Akademische verlagsgesellschaft, Frankfurt am Main, Germany.

GRIER, J. W., AND R. W. FYFE. 1987. Preventing research and management disturbance, p. 173–182. *In* B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC.

HASTÄDT, V., AND A. FIEDLER. 1991. Auswertung vierjähriger baumfalkenbeobachtungin den Kreisen königs wusterhausen und zossen im bezirk Postdam. Populationsökologie von greifvogel- und eulenarten 2:366–374.

MATTHYSEN, E. 1990. Behavioral and ecological correlates of territory quality in the Eurasian Nuthatch (*Sitta europea*). Auk 107:86–95.

MAYER-GROSS, H. 1972. The nest record scheme. British Trust for Ornithology, Tring, UK.

MIKKOLA, H. 1983. Owls of Europe. T and AD Poyser, Calton, UK.

MORATA, G. 1971. Observaciones sobre la reproduccion del Alcotan (*Falco subbuteo*). Ardeola 15: 37–48.

MÜLLER, T., AND C. ROHDE. 1991. Bestandssitation des Baumfalken (*Falco subbuteo*) im Donaudelta (Rumänien), p. 87–95. *In* R. D. Chancellor and B. U. Meyburg [EDS.], Birds of prey Bulletin No. 4. Lentz Druck, Berlin.

NEWTON, I. 1979. Population ecology of raptors. T and AD Poyser, Berkhamsted, UK.

NEWTON, I. 1991. Habitat variation and population regulation in Sparrowhawks. Ibis 133 (Suppl.):76–88.

OLENDORFF, R. R. 1993. Status, biology, and management of Ferruginous Hawks: a review. Raptor Res. Tech. Asst. Cen., Spec. Rep. U.S. Dept. Interior, Bur. Land Manage., Boise, ID.

PAIN, D. J., AND M. W. PIENKOWSKI. 1997. Farming and birds in Europe. The common agricultural policy and its implications for bird conservation. Academic Press, London.

PARR, S. J. 1985. The breeding ecology and diet of the Hobby *Falco subbuteo* in southern England. Ibis 127:60–73.

PARR, S. J. 1994. Population changes of breeding Hobbies *Falco subbuteo* in Britain. Bird Study 41: 131–135.

PREVOSTO, M. 1965. L'accrescimento del pioppo euroamericano I-214 nei diversi ambienti della pianura lombardo-piemontese in relazione alla spaziatura e al turno. Pubblic. Ente Nazionale Cellulosa e Carta, Rome.

PRINCE, P., AND R. CLARK. 1993. The Hobby's breeding range in Britain. What factors have allowed it to expand? British Wildl. 4:341–346.

PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137:S50–66.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

SERGIO, F., AND G. BOGLIANI. 1995. Selezione del sito di nidificazione nei pioppeti e correlazioni con il successo riproduttivo del Lodolaio *Falco subbuteo.* Avocetta 19:102.

SIEGEL, S., AND N. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman, New York.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity, p. 157–170. *In* B. A. Giron Pendleton, B. A. Millsap, K. W. Cline. and D. M.

Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC.
STEINKE, G. 1987. Zum vorkommen und zur fortpflanzung des Baumfalken *Falco subbuteo* (L.) im Kreis Zerbst. Populationsökologie von greifvogel- und eulenarten 1:207–216.
TOMASELLI, C., AND E. TOMASELLI. 1973. Appunti sulle vicende delle foreste padane dall'epoca romana ad oggi. Arch. Bot. Biogeogr. Ital. 49:85–101.
VIÑUELA, J., AND J. BUSTAMANTE. 1992. Effect of growth and hatching asynchrony on the fledging age of Black and Red Kites. Auk 109:748–757.
WENDLAND, V. 1953. Populationsstudien an raubvögeln. J. Ornithol. 94:103–113.