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Nest-hole selection as defence measure in breeding Swifts *(Apus apus)*

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Abstract — During the 1990-1991 breeding seasons we studied factors affecting Swift nest-hole selection, i.e. exposure, height, dimensions, type of holes and dispersion, in Pavia, Northern Italy. Exposure was not a significant factor, while in most cases Swifts nested at a height of 9-14 m in very small holes, often barely large enough to let them in. Holes were the sites selected in most cases; however a number of Swifts used the spaces under tiles, and a small number nested under eaves or behind shutters. Swifts were found nesting at 1-2 m maximum distance, confirming that nest-aggregation is another important factor in hole selection.

Introduction

The breeding range of the Swift, *Apus apus,* covers the Western Palearctic from North Africa to the Polar Arctic Circle (Cramp 1985). In Italy it is present from March-April to July-August (Farina 1980, Koller 1982, Boano 1988, Grandi and Nova 1990). It mainly breeds in colonies, selecting holes as nesting sites, where House Sparrows *Passer domesticus,* Starling *Sturnus vulgaris* and Rock Dove *Columba livia* also nest (Quadrelli 1985). Holes are occupied by the adults, but some of the young may also try to build a nest, even if they are immature (Weitnauer 1947, Magnusson and Svardson 1948, Glutz and Bauer 1980); otherwise they rest in the air (Poncy 1928, Weitnauer 1960). In Italy the Swift has been little studied (Farina 1980, Quadrelli 1985), whereas its relative, the Pallid Swift *Apus pallidus,* has received more attention, due to its rareness (Boano 1979, Cucco and Malacarne 1987, Malacarne *et al.* 1989).
The aim of our study was to investigate the main factors affecting nest-site selection and the strategies adopted by Swifts to avoid predation.

Methods

The study was carried out from April to July in 1990 and 1991 in the centre of Pavia (Northern Italy). The town is characterized by old buildings (1100-1800 A.D.), avenues, parks, private gardens, and is located along the River Ticino. The area has a sublittoral continental temperate climate; during Swift breeding season the monthly average temperature varies from 13°C (April) to 25°C (July) and the monthly average precipitation is 65 mm. A census of the colonies breeding in the study area (2 km^2) was carried out both years in the same breeding phase (early July) and at the same time of day (11-13 h). In this period the air-ranges of different colonies showed no overlap and stranger individuals were drive off. So that, the consistency of the colonies was calculated by estimating the flocks flying over buildings where Swifts were seen to enter or exit from holes. Type of building and of hole selected were recorded for each colony. An intensive study area (the Visconti Castle), was selected and monitored in both breeding seasons in order to investigate nest height, dimensions and distribution. The Visconti Castle is a fourteenth century brick building, with three facades (West, South and East) and two square-based towers. Its walls are characterized by 2272 scaffolding holes, normally 15x15 cm, 1375 on the three facades and 897 on the two towers. Drawings of the facades and towers were made, indicating the localization of the scaffolding holes. These were then classified as "obstructed", holes whith entrance that had been partially blocked, on average 3x3 cm, and "unobstructed", on average 15x15 cm, using binoculars. All the holes were 50-100 cm deep. There were 99 obstructed and 2173 unobstructed holes. Obstructed holes were distributed randomly between unobstructed ones. There are 30 lines of scaffolding holes, and the facades were subdivided into 10 levels: each level consisted of three horizontal lines of holes and was 2.4 m high. The first level started at 4 m. We performed the χ^2 goodness of fit test on the proportions of available and used holes in order to evaluate statistically the differences in the height, dimensions and exposure of the holes selected by the

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Swifts; effective nest-holes were only those into which a Swift entered completely, at least twice in more than a fortnight. Where a significant difference between availability and actual use of holes at various heights, dimensions and exposure was found, Bonferroni's simultaneous confidence intervals analysis (Neu et al. 1974, Alldredge and Ratti 1986) was used to determine which were actively selected and which rejected:

$$Pi - Za/2k \sqrt{Pi\,(1-Pi/n)} < P < Pi + Za/2k \sqrt{Pi\,(1-Pi)}/n$$

where:
Pi = percentage of nests observed at an i-th height
a = probability level (95%)
k = facade level
Z = standard table value of one tailed-probability integral of a/2k
n = total number of observations.

We adopted the "Nearest-Neighbour method" (Clark and Evans 1954) to evaluate nest distribution, comparing the observed distances between nearest nests with those expected from a Monte Carlo simulation, carried out on the number of nests found in 1990 and 1991 (Bekoff and Mech 1984); one thousand random distributions were effected.
The G test (Sokal and Rohlf 1981) was used to evaluate statistically the differences between observed and expected distances subdivided into six classes of frequency (0-0.5, 0.5-1, 1-1.5, 1.5-2 m ...):

$$G = 2\Sigma f_o \ln (f_o/f_e)$$

where f_o is the observed frequency of distances subdivided into six classes and f_e the expected frequency of distances.

Results

Twenty-six colonies were censused in each breeding season, and the total number of Swifts in the centre of Pavia varied from 1600 to 2400 individuals

Table 1. Estimated number of Swifts in the colonies of the centre of Pavia (Building: C = church, CA = castle, B = bridge, H = house, M = Monumental building, D = dovecote for Swifts, T = tower; Nest-site: e = eave, h = hole, t = tile).

Colony	Building	Nest-site	number of individuals			
			min.		max.	
			1990	1991	1990	1991
1 Cathedral	C	h-t	300	300	500	500
2 Visconti Castle	CA	h	150	150	200	200
3 Leonardo da Vinci Tower	T	h	150	150	150	150
4 Belcredi Tower	T	h	150	150	150	150
5 St. Francesco	C	h-t	150	150	150	150
6 St. Maria del Carmine	C	h	100	150	100	150
7 St. Dalmazio Tower	T	h	80	100	150	150
8 St. Michele	C	h-t	70	70	100	100
9 St. Luca	C	h	50	50	80	80
10 St. Teodoro	C	t	50	50	80	80
11 Borromeo College	M-T	e-h	50	50	80	80
12 Covered Bridge	B	t	40	40	70	70
13 St. Maria di Canepanova	C	h	40	40	50	50
14 St. Tommaso	C	h	40	40	50	50
15 Pharmacology Institute	H	t	30	30	50	50
16 P. Calcinara	H	t	20	20	50	50
17 Castiglioni College	M	t	10	10	50	50
18 Cairoli College	M	h	10	10	50	50
19 St. Francesco da Paola	C	t	10	10	50	50
20 St. Primo	C	h-t	10	10	50	50
21 St. Gervasio & Protasio	C	h-t	10	10	50	50
22 Ugo Foscolo School	H	t	10	10	50	50
23 St. Pietro in Ciel d'Oro	C	e-t	10	10	30	30
24 Scaldasole dovecote	D	h	10	10	30	30
25 St. Marino	C	h-t	10	10	20	20
26 Piazza della Posta Tower	T	h	10	10	10	10
Total			1560	1630	2390	2440

including non-breeders (Tab. 1). Eleven (42.3%) colonies were located exclusively inside holes in buildings, 7 (27%) under the tiles, 6 (23.1%) utilized holes and tiles of the same building; finally, only 2 colonies (7.7%) used the spaces under eaves. Some Swifts bred isolated using the spaces behind shutters. The colony breeding at the Visconti castle consisted of 150-200 Swifts in both the years of study. In 1990, 68 Swift pairs nested inside the holes, in 1991 the number was 63. Exactly 50% of the holes selected in 1991 had also been selected the year before. The data collected showed that nest-hole selection is independent of exposure (Tab. 2), most holes selected were small holes, which is significantly more than the big ones ($\chi^2 = 1333.06$, d.f. = 1, $p<0.001$). In 1991 there was a decrease in the percentage of small holes used; however, they were significantly by selected again ($\chi^2 = 370.5$, d.f. = 1, $p<0.001$) (Tab. 3). In certain parts of the building higher concentrations of pairs were observed. In both years the birds significantly selected holes at medium height levels ($\chi^2 = 59.3$ d.f. = 9, $p<0.001$ in 1990; $\chi^2 = 31.1$, d.f. = 9, $p<0.001$ in 1991). Bonferroni's simultaneous confidence intervals analysis showed that a height from 8.8 to 13.6 m was actively selected, while levels under 6 m and over 23 m were rejected (Tab.4). Aggregation of the Swift nests was confirmed: in 1990 no distance observed was greater than that to be expected from a Monte Carlo simulation (1000 dimensions), the probability thus being less than 0.001; the G test confirmed the result (G = 40.96, d.f. = 5, $p<0.001$). In 1991 only 3 nests were located at a greater distance than that to be expected from the same simulation ($p<0.003$), and the G test was again significant (G = 15.37, d.f. = 5, $p<0.01$).

In 1990, 69.1% of the nests were located within 1 m of another nest and 82.3% within 1.50 m; in 1991, 60.3% of the nests were less than 0.5 m from another nest and 87.3% less than 2 m (Tab. 5 and Fig. 1).

Table 2. Nest exposure at Visconti castle (χ^2 Test).

exposure	available holes	occupied holes 1990	occupied holes 1991
East	600	18	12
South	1002	30	35
West	670	20	16
significance level		ns	ns

Table 3. Hole dimension in nest-hole selection (χ^2 Test).

dimension	available holes	occupied holes 1990	occupied holes 1991
big holes	2173	4	29
small holes	99	64	34
significance level		P<0.001	P<0.001

Discussion

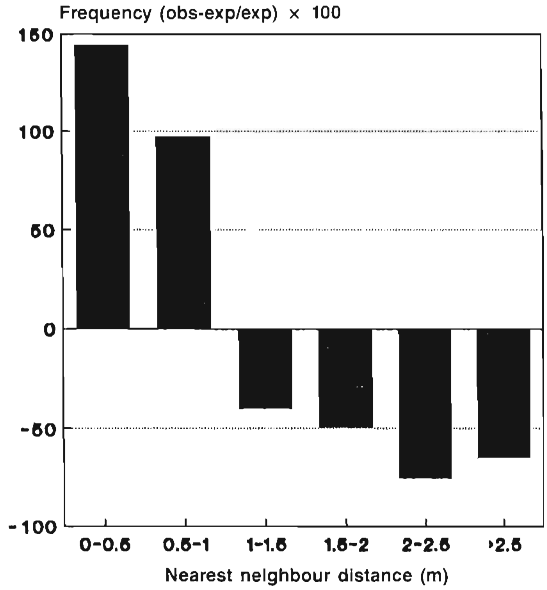
Holes are considered the safest type of nest-sites, especially for the young trying to leave the nest while still unable to fly (Gory 1987), and this should explain the preference of the Swifts for this kind of cavity. However, in other areas (Gibraltar) Swifts mainly used spaces under eaves to breed (63% of nests), while holes in the buildings were scarcely occupied (2%), and the same was observed for Pallid Swifts (Finlayson 1979, in Cramp 1985).

Table 4. Results from Bonferroni's intervals analysis for height levels in nest-hole selection (χ^2 Test).

height (m)		available holes	expected as occupied 1990	expected as occupied 1991	occupied holes 1990	occupied holes 1991	significance level 1990	significance level 1991
I	4.0-6.4	340	10.2	9.4	2	1	-*	-*
II	6.4-8.8	382	11.4	10.5	7	10	ns	ns
III	8.8-11.2	351	10.5	9.7	26	21	+*	+*
IV	11.2-13.6	376	11.2	10.4	25	18	+*	ns
V	13.6-16	372	11.1	10.3	8	10	ns	ns
VI	16.0-18.4	86	2.6	2.4	0	1	-*	ns
VII	18.4-20.8	88	2.6	2.4	0	1	-*	ns
VIII	20.8-23.2	100	2.9	2.8	0	1	-*	ns
IX	23.2-25.6	92	2.7	2.5	0	0	-*	-*
X	25.6-28	85	2.5	2.3	0	0	-*	-*
significance level					P<0.001	P<0.001		

* marks a significance level of p< 0.05; + indicates preference, - indicates avoidance.

Figure 1. Percentage differences between observed and expected frequencies, expressed as: [(observed-expected)/expected] x 100, of the nearest-neighbour distances between nests. Left: 1990 season. Right: 1991 season.



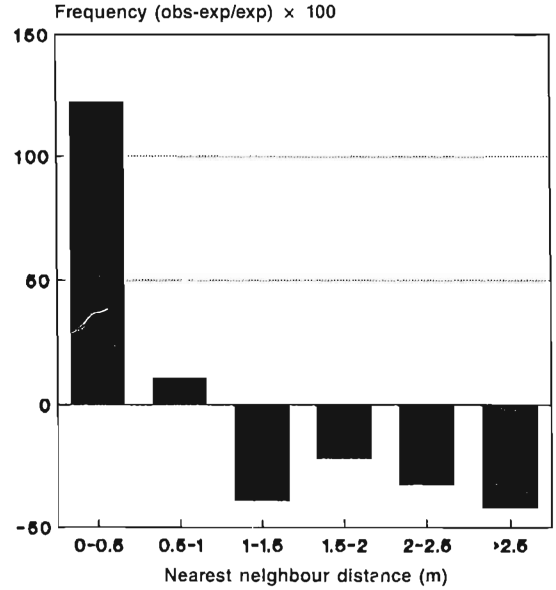


Table 5. Nest aggregation factor in nest-hole selection (G Test).

nest-hole distance classes (m)	distance frequency expected 1990	distance frequency expected 1991	distance frequency observed 1990	distance frequency observed 1991
0-0.5	7.4	9	18	20
0.5-1	14.7	16.3	29	18
1-1.5	14.9	14.7	9	9
1.5-2	11.8	10.2	6	8
2-2.5	8	5.9	2	4
>2.5	11.3	6.9	4	4
significance level			P<0.001	P<0.01

Probably this difference depends on the local availability of different nest-sites and the presence in Pavia of many ancient buildings with scaffolding holes may justify the preference for holes showed by Swifts breeding in this town.

Boano (1979) found that Pallid Swifts breeding in a colony in Torino mainly used holes 3-4 m high, while in the same building Swifts occupied higher levels, reaching the top of the towers. Cucco and Malacarne (1987) observed 50% of the pairs of this Pallid Swift colony selecting holes 8-13 m high, while Swifts built their nests higher in the same building. In our colony, Swifts occupied holes at 9-14 m levels, which is comparable to the height observed by Cucco and Malacarne (1987) for the Pallid Swift rather than for the Swift. Nest-hole competition between the two species could lead Swifts to nest higher when the Pallid Swift is present; otherwise Swifts would occupy the same levels selected by the Pallid Swift. Some degree of interspecific competition in nest-site selection might in fact be involved; recently, along the Gargano Promontory coasts, Brichetti *et al.* (1988) found that the two species were aggregated in only 5 of 39 colonies censused, and Swifts were few in mixed colonies. Indeed they concluded that the presence of other species of Apodidae in a cliff can limit the colony size of Swifts. However, the prevalence of the Pallid Swift in the competition might simply be due to a chronological factor, since it reaches the breeding areas slightly earlier than the Swift (Boano 1979). Nest-aggregation, yet found in Pallid Swift colonies

(Cucco and Malacarne 1988), has been confirmed in Swifts also, but, lacking data on communal breeding in this species, its function remains to be clarified.

Generally gregariousness is considered to be a form of protection against predators acting either by a "dilution" effect of group reducing probability of an individual being caught (Hamilton 1971) or by an enhancement of active defence. In Swifts, such a behaviour may be effective against diurnal predators catching them or their offsprings in fly like *Falco subbuteo* and *Accipiter nisus* do (Daanje 1944, Slijper 1948, in Cramp 1985) and may have therefore this kind of adaptive value in natural habitats. But in urban areas, this strategy may be ineffective against predators which prey on Swifts directly from the nests, moreover against nocturnal, resident and high memory performances predators as Tawny Owls, *Strix aluco*. In fact, 3 pairs of Tawny Owls preyed on Swifts breeding in the centre of Pavia and Swifts constituted 30% in weight of the spring diet of the pair preying on the Visconti Castle colony (Galeotti *et al.* 1991). Indeed Swift colonies are optimal and seasonally predictable feeding patches for breeding Tawny Owls, providing suitable prey (40 g) with low energy loss, since the owl's perches in Pavia are located very close to the Swift colonies. In this conditions, nest-aggregation seems to be a bad defence strategy, since it attracts potential predators and enhances their succes rate; however it is maintained, suggesting that nest-aggregation in Swifts, far from primary serve as defence, might on the contrary enable them to exchange crucial information about food sources. The diet of Swifts, based on ephemeral, scattered and unpredictable resources as flying insects, and the social modality of clumped arrivals and departures from nests we observed (Galeotti and Colombo, unpubl.data) support the information-centre hypothesis (Ward and Zahavi, 1973). If nest aggregation is adaptive in this way, selection of small holes could be a good answer in the "arms-race" beetwen Swifts and predators. Small holes, i.e. holes with a very tiny slit for entrance, are an inexpensive passive measure of defence, effective against all potential predators. The Hooded Crow *Corvus corone cornix*, was also observed exploring Swift nest-holes, with a high frequency of visits (about one every 15 min). The Hooded Crow explored only the big holes by standing at the entrance or going inside; it often visited 3-4 holes at a time in this way, and then flew away. When a Hooded Crow approached the holes, most of the Swifts rose to a high altitude in absolute silence and flew in a single flock or in two big formations. Only 3-4 Swifts remained at hole height, weakly mobbing the Hooded Crow until it flew away from the colony. The behaviour described was observed whenever a Hooded Crow explored the holes and was constant in June-July, while in April-May the Swifts' reaction was less perceptible. Even without observing the Hooded Crow actually preying on eggs or young, predation can be assumed on the basis of the Swifts' particular behaviour. In this case too, selecting small holes functions against the predator.

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Riassunto — Durante le stagioni riproduttive 1990-1991 abbiamo studiato i fattori che influenzano la scelta del sito riproduttivo del Rondone in una colonia localizzata sulle facciate del Castello Visconteo di Pavia (Nord Italia). Sono stati considerati esposizione, altezza, dimensioni e tipo di dispersione delle cavità occupate dalle coppie riproduttive. Mentre l'esposizione non influenza in alcun modo la scelta del sito, l'altezza e le dimensioni dei fori di ingresso costituiscono invece fattori importanti. I rondoni selezionano infatti attivamente fori di piccole dimensioni (3x3 cm) appena sufficienti a consentire il passaggio, posti ad altezze comprese tra i 9 e i 14 m . I nidi attivi non sono distribuiti in modo regolare o casuale, ma sono concentrati in gruppi; le distanze tra i nidi sono comprese tra 0.5-2 m. Le piccole dimensioni dei fori d'ingresso dei nidi costituiscono con ogni probabilità un adattamento alla predazione. Sia l'Allocco che la Cornacchia grigia esplorano infatti sistematicamente i buchi delle facciate e, nel caso dell'Allocco, il prelievo annuale di un notevole numero di individui adulti è documentato con certezza.

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