A Barn Swallow *Hirundo rustica* roost under attack: timing and risks in the presence of African Hobbies *Falco cuvieri*

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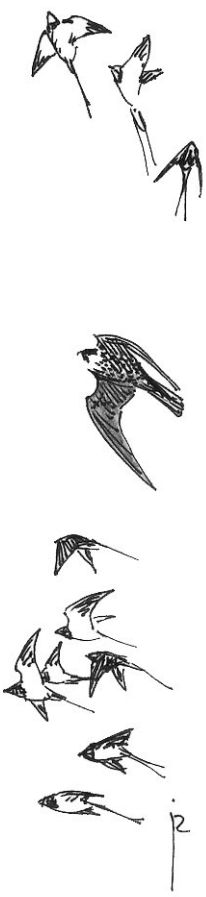

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A large Barn Swallow *Hirundo rustica* roost in *Pennisetum*-covered clearings amid rainforest in SE Nigeria attracted at least eleven species of avian predators. Departure and arrival of Swallows at the roost was highly predictable and synchronised: >90% of up to 1.5 million birds ascended and descended within 10 min around sunrise and sunset, respectively, in spectacularly fast and dense masses. African Hobbies *Falco cuvieri* timed their presence and behaviour in conjunction with the Swallows, arriving 2–14 min before departure or arrival of the first Swallows. Overall success rate of hunts was 38%, and independent of hunting height, hunting mode and time relative to sunrise or sunset. Hunting success showed a strong quadratic relationship with flock size, and was highest in attacks on small flocks of 1–50 Swallows. The hunting window, i.e. the period that Swallows were present and airborne, amounted to 20–40 min per twilight cycle. Swallows reduced predation risks by (1) roosting in huge numbers, (2) timing arrival and departure in a short period around sunset and sunrise, (3) making a fast and synchronised descent and ascent (swamping aerial predators) and (4) – possibly – keeping their weights low until the very end of the moulting cycle (when body mass increases in anticipation of migration). Assuming the seven local African Hobbies succeeded in capturing a Swallow each twilight period, we estimate the number of Swallows taken per wintering period at 2500. This is a small proportion in comparison with the depredation by local people that have been reported to collect more than 100 000 Swallows each year.

Key words: *Hirundo rustica* – *Falco cuvieri* – temporal predation pattern – anti-predator strategies – communal roosting – Nigeria

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INTRODUCTION

Millions of Barn Swallows *Hirundo rustica* leave Europe in late summer and early autumn, to spend the winter in Africa. In tropical and southern Africa, the species is highly gregarious and uses reedbeds, fields of sugar cane, maize, elephant grass and similarly structured vegetation to roost in flocks of up to several millions (Curry-Lindahl 1981, Keith *et al.* 1992). During our quest for Barn Swallows in various parts of Africa, all roosts located were being exploited by avian predators

(Bijlsma *et al.* 1994, van den Brink *et al.* 1997, 1998, 2003). Several roosts in Botswana, varying in size between hundreds and 2.7 million Swallows, attracted Gabar Goshawk *Micronisus gabar*, Little Sparrowhawk *Accipiter minullus*, Red-necked Falcon *Falco chicquera*, Eastern Red-footed Falcon *F. amurensis*, Eurasian Hobby *F. subbuteo*, Lanner Falcon *F. biarmicus*, Peregrine *F. peregrinus* and Barn Owl *Tyto alba* (Bijlsma *et al.* 1994, van den Brink *et al.* 1997, van den Brink *et al.* 2003). Roosts of up to 11 000 Swallows in Ghana were attended by Eurasian Marsh Harrier *Circus aeruginosus*, African Hobby *F. cuvieri* and Grey Kestrel *F. ardosiaceus* (van den Brink *et al.* 1998).

The Swallow roost near Boje-Ebok in the Cross River State of south-eastern Nigeria attracted much attention when it was detected that human depredation alone accounted for the annual loss of 100 000 or more Swallows (Ash 1995, Loske 1996). We studied this roost in early 2001, when some 1.5 million Swallows were present. Although human predation had temporarily come to a halt, the site still swarmed with predators (Bijlsma 2001, 2002).

Raptor concentrations in Africa are well-known phenomena, often associated with weather-related swarming of alate termites, locust outbreaks and bush fires. Such irregular and sometimes infrequent boosts of food supply invariably attract a mixture of African and Palearctic raptors (Brown 1971). Large Swallow roosts, on the other hand, are predictable in space and time, and act like a magnet on – mostly local – predators. Spatial and temporal patterns of danger are likely to impact habitat use, evolution of movements, annual and daily cycles (Butler *et al.* 2003) and behaviour of prey species (Neill & Cullen 1974, Milinski 1984, Lima 1998). Furthermore, prey species living in an environment riddled with predators face a trade-off between starvation and predation risk (McNamara & Houston 1990, Lilliendahl 1997, van der Veen 1999, Piersma *et al.* 2003). Predators, on the other hand, are not unresponsive abstractions, but react to the behavioural plasticity of their prey, a little studied aspect of predator-prey interactions (Lima 2002, Cresswell & Quinn 2003).

In this observational study we describe the interactions between roosting Swallows and African Hobbies, a swift aerial predator capable of hunting in near-darkness. We were interested in the strategies of African Hobbies exploiting this predictable food bonanza during the short bouts of availability at dusk and dawn. Further, we investigated in which way Swallows were able to reduce predation risks posed by African Hobbies (embedded in a multipredator environment).

STUDY SITE AND METHODS

The study site lies in the foothills of Afi Mountain on the Obudu Plateau (6°38' N, 9°00' E), situated between 200–500 m above sea level. It is one of the few pockets of primary rainforest left in Nigeria (extending into Cameroon). The area is rugged and densely forested, except for the valleys where oil palms, cocoa, banana, plantain and yam are cultivated in forest clearings. Part of the hill side east of the village Ebbaken-Boje had been cleared of forest and is now covered with extensive areas of elephant grass *Pennisetum* spp (Fig. 1).

Visibility was restricted (800–1500 m) during the *Harmattan*, the dry, gusty and dust-laden wind from the Sahel and Saharan desert that dominated the period between 4 and 17 February. This was exacerbated by the smoke of numerous bush fires. In early February, visibility was better (up to 5 km). Cloud cover was non-existent until 18 February. From then on, some cloud formation occurred in the morning with very slight rainfall on 20 February. Maximum daily temperatures in the shade varied between 31 and 40°C, minimum temperatures between 14 and 21°C (just before sunrise).

The Swallow roost was under surveillance from 18 January through 20 February 2001. In early morning and evening, we spent between one and four hours in catching and handling Swallows at the roost in 4–5 m high *Pennisetum* grass. Mist nets were put up in the elephant grass and opened 1.5–2 h before departure or arrival; tapes with full song were played non-stop to lure Swallows into

Figure 1. View from the valley floor towards the *Pennisetum*-covered slopes of Afi Mountain, the main Swallow roost of the Boje-Ebok region in SE Nigeria, February 2001 (B. van den Brink).

the nets. Captured Swallows were aged and sexed (if possible), and ringed and released on the spot except for a random sample of birds that were processed later to obtain biometrics (n = 530; Table 1). We measured wing length (flattened and straightened), length of 8th primary, tarsus, fat score (scale 0–5), body moult, primary moult score (0–5), body mass (digitally and with spring balances) and depth of tail fork (for details, *cf.* van den Brink *et al*. 1997).

In early morning swallow flocks were counted on a minute-by-minute basis upon departure, until all Swallows had left the roost. Roost size was determined by totalling these figures. Flock size was impossible to determine during mass departure, when a seemingly endless stream of Swallows left the roost. Under such circumstances, numbers departing per minute were used as flock size substitutes. In the evening, Swallows flocked together in huge swarms over the roost, to descend *en masse* during twilight; assessing flock size was then impracticable.

The roost of up to 1.5 million Swallows at Boje-Ebok was exploited by at least three Yellow-billed Kite *Milvus migrans parasitus*, an adult male Eurasian Marsh Harrier, one pair of African Harrier-hawks *Polyboroides typus pectoralis* with a single fledgling, two Red-breasted Sparrowhawks *Accipiter toussenelii*, a Shikra *A. badius*, up to seven African Hobbies, an adult Lanner Falcon, a Barn Owl, two Common Scops Owls *Otus scops*, a pair of African Wood Owls *Strix woodfordii* and a Senegal Coucal *Centropus senegalensis* (Bijlsma 2001, and unpublished). Except for African Hobbies, the hunting strategy of avian predators was to hug the roost site with low-level flights,

Table 1. Body mass, fat score and primary moult score of Barn Swallows mist-netted at the Boje-Ebok roost in SE Nigeria in 2001.

Date	Sample size	Mass (g)		Fat score		Primary score	
		Mean	SD	Mean	SD	Mean	SD
January 18	18	18.1	1.20	2.00	0.69	29.9	5.89
January 20	15	16.7	1.04	1.53	0.64	32.9	6.60
January 25	19	16.1	0.66	0.53	0.51	33.3	5.52
January 31	18	19.5	2.60	3.06	1.06	32.7	6.34
February 1	40	18.8	1.42	2.05	1.38	35.4	6.86
February 2	2	18.6	0.90	1.00	0.00	36.0	7.07
February 3	22	17.7	1.18	1.05	1.13	38.4	5.61
February 5	28	15.9	0.77	0.00	–	39.8	4.07
February 6	25	15.8	1.11	0.00	–	39.6	5.65
February 7	28	15.8	0.70	0.00	–	38.7	6.27
February 9	30	15.8	0.74	0.00	–	38.5	5.58
February 10	21	15.6	0.79	0.43	1.96	39.0	5.01
February 11	25	15.3	1.04	0.00	–	39.1	4.53
February 12	26	15.4	0.78	0.00	–	39.3	4.53
February 13	21	15.4	0.73	0.00	–	41.7	2.67
February 14	25	15.1	0.70	0.00	–	40.7	4.69
February 15	49	15.3	0.94	0.00	–	40.3	4.81
February 17	23	17.1	0.91	0.00	–	41.4	4.27
February 18	25	17.3	1.26	0.08	0.28	42.0	3.37
February 19	25	18.0	1.03	0.68	0.90	41.1	3.91
February 20	28	18.0	1.19	1.04	0.96	40.4	4.64
February 21	20	17.5	1.09	0.35	0.88	42.3	2.75

either trying to flush roosting Swallows (kite, harrier, Accipiters) or to capture Swallows sitting near gaps in the vegetation (owls, coucal). Prey remains of ten Swallows (5 juveniles, 5 full-grown) collected at the roost on 11 February were probably victims of the roost-hugging bunch of the raptor guild; the falcons plucked their prey away from the roost in trees.

At dawn, avian predators and their activities were recorded from darkness onwards till all Swallows had departed the roost (1–1.5 h), normally while looking from the valley floor into an easterly direction. At dusk, observations started 1–1.5 h before sunset and lasted till darkness. We recorded raptor species (age and sex if possible), modes of flight, timing and mode of hunting and hunting success. Flying height was estimated as low (<50 m), mid-high (50–100 m), high (100–500 m) and very high (>500 m). Four modes of flight were recognised, i.e. speeding, leisure active flight, soaring (various heights) and cruising (high up, using slow wing action). Such flights could switch into a hunt, i.e. a directed attack at an identifiable bird or flock including one or more passes, stoops or swoops. The end of a hunt was visible as a switch in flying mode and flight direction, often from pursuit into a more leisurely flight with gliding intervals. Any hunt initiated after such a switch was recorded as another hunt. This definition is in accordance with that of Dekker (1980) and Cresswell (1996). Catching hold of a prey was recorded as a capture; actual kills were rarely witnessed, unless plucking started in the air.

Hunts were tallied as full pursuit (speeding with fast wing action), shallow dive (<30°) and stoop (>30°); the latter was sometimes accompanied by short bouts of speeding, audible as a ripping sound. Out of 171 hunts recorded during 18 days, the outcome was established in 66 cases (56 at dawn, 10 at dusk). Hunts with unknown outcome were similarly distributed over the observation periods as hunts with known outcome; no difference either was found in flying mode or flying height. We therefore believe that our sample of hunts with known outcome is not biased in any direction.

In addition to roost observations, from 1–20 February 97.5 observation hours were spent in systematically recording raptor activities using focal watches of 1–4 hours, mostly between 7.30 and 17.45 hr from vantage points 100–150 m above the valley floor (Bijlsma 2001, 2002).

We used logistic regression (PROC CATMOD; SAS Institute 1989) to test for differences in hunting success in relation to the following parameters: flock size of Swallows, minutes from sunrise /sunset (continuous variables), sunset/sunrise, hunting mode, number of falcons involved (solitary or more than 1), hunting height (class variables). As we expected a bi-directional influence of Swallow flock size on hunting success, a quadratic effect was included in the tests. The initial model included all parameters of interest, and non-significant terms were successively dropped from the model (backward procedure). Means are given ± 1 SD.

RESULTS

Roosting Barn Swallows: mass and moult

During daytime, very few Swallows were observed in the Boje-Ebok area. Low-level foraging was occasionally recorded in the valley between Ebbaken and Enji, especially in early morning, and involved small groups on the move. From 18–20 February, between 10:00 and 12:30 h, small flocks of 10–55 European Swallows were observed passing at mid-high to high altitudes in various directions, often together with Swifts *Apus apus*. Such movements were not recorded in the first half of February. The passage converged with the change of a *Harmattan* spell (dry dust-laden winds from the north) into damp weather with cloud formation from the south. A distinct increase in the average mass and fat load of Swallows captured at the roost (Table 1) coincided with this weather-shift, after a ten-day period of catching Swallows with low masses and no fat. The primary moult score increased from <30 in mid-January to >40 in late February (Table 1), i.e. from moulting primary 5/6 to having almost finished primary moult (P9 growing or renewed). Overall, adults were heavier (on average 18.1 ± 2.31 vs. 16.6 ± 1.69 g, 44 adults respectively 254 juveniles) and more advanced in primary moult than juveniles (on average one primary ahead). Age categories have been pooled in Table 1, as ageing became increasingly problematic in the course of February in the wake of an increasing proportion of birds having finished their moult.

Timing and behaviour of Swallows at the roost

The behaviour of Swallows at the roost was synchronised and predictable. At the precise start of civil twilight in early morning, 20 minutes before sunrise, Swallows started bill-snapping and twittering. In the following minutes the tension built up and singing intensified in strength, an enchanting moment in a rainforest setting. Many Swallows started preening, wing-stretching and fluttering. The first Swallows normally departed from the roost between 0 and 9 minutes before sunrise (on three days 1–3 minutes after sunrise), to be followed by mass departure on average 5.0 minutes later (Fig. 2). Overall departure took between 20 and 49 minutes (on average 31 ±8.5 minutes, n = 15 days between 4 and 20 February), but 90% of the Swallows departed in less than ten minutes (Fig. 3). In general, Swallows exhibited two ways of departing, i.e. (a) “rolling downhill” in fast flight, hugging the elephant grass or using openings in the grass to fly even lower, and (b) flying straight up, as fast and as steep as possible, sometimes using tight spiralling to gain height. The latter

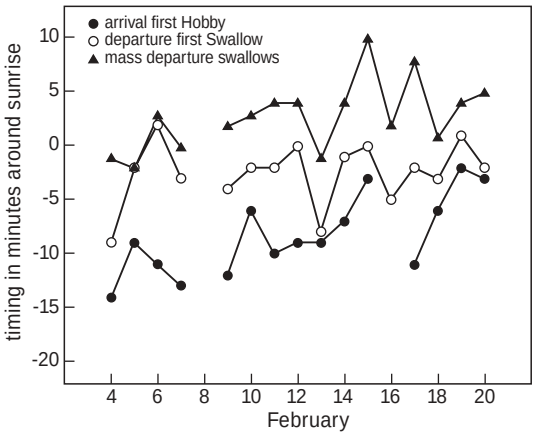

Figure 2. Timing in relation to sunrise (= 0) of African Hobbies and Barn Swallows from 4 to 20 February 2001 at the Boje-Ebok roost in SE Nigeria.

involved >95% of all birds, whereas Swallows started "rolling downhill" when low-flying falcons suddenly appeared, perhaps in combination with the activities of other raptor species. In both cases, the Swallows left the area of the roost at full speed, with flocks dispersing when they had distanced themselves from the roost.

In the evening, the same routine was followed in reverse order. The first Swallows arrived on average 19.7 ± 7.9 minutes before sunset (range 11–35 minutes, n = 6 days), but 92% were recorded in the first 9 minutes after sunset. By ten minutes after sunset, almost all Swallows had settled in the elephant grass. Between arrival and final descent of the majority of birds, on average 25.5 ± 4.5 minutes passed (range 20–33 minutes, n = 6 days). Arriving birds flew very high, almost invisible against the darkening sky. The descent was spectacular. Dense throngs of Swallows "rained" downwards, diving into the roost at great speed. Within a couple of minutes, hundreds of thousands of Swallows had entered the roost. Most birds attempted to settle in the elephant grass as high uphill as possible.

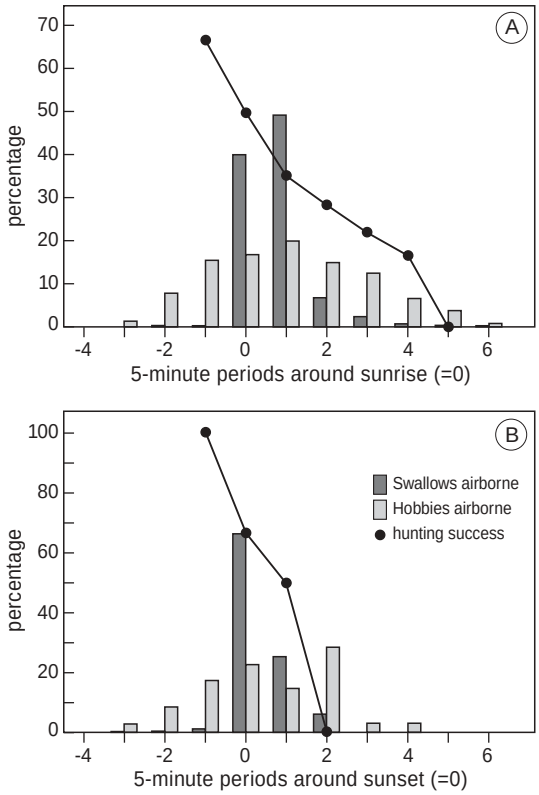

Figure 3. Proportion of Swallows departing or descending relative to sunrise (A) and sunset (B) at the Boje-Ebok roost in February 2001, compared with proportion of African Hobbies airborne. The declining trend in hunting success during mass departure and descent of Swallows is non-significant (Table 3).

Hunting strategy of African Hobbies

African Hobbies hunted either singly (84.8%) or cooperatively in twos (13.6%) or threes (1.5%, n = 66 hunting flights with known outcome). Low-level flights were common practice (54.5% lower than 50 m), especially at dawn (Table 2). High flights were typical in the evening, because the gathering Swallows reacted to the appearance of avian predators by gaining height and swarming in dense masses. Early morning hunting of Hobbies was very different, as the Swallows had to ascend from ground level, and responded to the-presence of low-flying Hobbies by leaving the roost

Table 2. Hunts with known outcome and kills (vertebrates only) of African Hobbies in relation to time of the day (full hours, local time) and flying height at Boje-Ebok, 1–21 February 2001.

Time of day	<50m	50–100m	100–500m	>500m	Sum
Morning (6–7 h)					
Hunts	33	20	3	0	56
Kills	14	6	1	0	21
Daytime (8–17 h)					
Hunts	0	0	0	0	0
Kills	0	0	0	0	0
Evening (18 h)					
Hunts	3	3	3	1	10
Kills	2	1	1	0	4

Table 3. Logistic regression of hunting success of African Hobby attacking Barn Swallows in relation to flock size of Swallows, number of falcons hunting together, hunting height, hunting mode and speed, and time relative to sunrise and sunset.

Parameter	Change in deviance	*df*	*P*	Coefficient
Constant	–	1	–	–0.356
Flock size	3.94	1	<0.05	1.908
Flock size^2	7.98	1	<0.005	–0.918
Number of falcons	1.96	1	0.16	–
Height	3.03	4	0.55	–
Time to sunrise/sunset	0.05	1	0.83	–
Hunting mode	0.05	2	0.97	–
Hunting speed	2.12	2	0.35	–

at high speed and hugging the contours of the *Pennisetum* vegetation until the forest edge was reached. Such flocks were attacked in full level pursuit or by using repeated short dives, causing the Swallows to scatter in all directions. When Swallows left the roost in steep ascent, Hobbies attacked by stooping from higher up, with an upward swoop at the end of a dive.

Timing of African Hobbies

In early morning African Hobbies arrived during civil twilight, either cruising high in the air or speeding along the slopes of the hill with an occasional dip into gaps of the elephant grass, perhaps to frighten Swallows into flight. The first African Hobby arrived 2–14 minutes before sunrise (mean 8.3 ± 3.6 minutes, n = 15), and 3–13 minutes before the first Swallows departed from the roost (mean 6.4 ± 2.9 minutes, n = 15 days) (Fig. 3A). Hobby presence peaked in the 30 minutes around sunrise, and tapered off after the majority of Swallows had disappeared.

During daytime (8–17 h local time), when Swallows were absent, we observed only 17 African Hobbies (0.5/100 min), opposed to 239 records in early morning (34.4/100 min) and 39 in the evening (6.8/100 min). Most of these birds were soaring and cruising at high altitudes while hawking insects; we never witnessed attempts to catch birds during daytime.

In the evening the first Hobbies arrived at the roost 15–20 minutes before sunset, when Swallows were normally still absent; 83% of Hobby flights were recorded from 7 min before sunset till 11 min after sunset (Fig. 3B). Flights during civil twilight may have been under-recorded because our attention focused on catching Swallows from sunset onwards.

Hunting success of African Hobbies

Overall success rate of hunts was 37.9% (25 out of 66 attacks). African Hobbies were attacking solitary Swallows as well as flocks from 2 to 15 000 Swallows. Hunting success was strongly dependent on the flock size of the Swallows (Table 3). The quadratic relationship between hunting success and flock size indicates that falcons were most successful when attacking flocks of intermediate size, 2–50 birds (Fig. 4). None of the other parameters had a significant effect on hunting success, neither while allowing for flock size effects nor when testing separately. There was some evidence that Hobbies hunting cooperatively were more successful in catching Swallows than birds hunting singly (50%, n = 10, and 35.7%, n = 56, respectively).

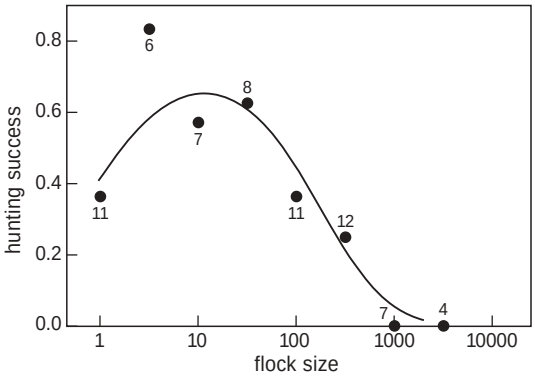

Figure 4. Hunting success of African Hobbies in relation to flock size of Swallows. Numbers indicate sample sizes. Flock size is on a logarithmic scale. Statistics are given in Table 3.

DISCUSSION

Strategies to capitalise on a food bonanza: timing and hunting efficiency

African Hobbies, being aerial hunters, could only effectively attack Swallows at the roost when these were present and airborne, i.e. in the constricted window of 30 minutes around sunset and sunrise. The fact that Hobbies arrived at the roost 2–14 minutes before the Swallows started to fly in or out seems to indicate that they anticipated the timing of Swallows. Mass departure involved huge numbers and dense flocks spiralling straight up in just a matter of minutes. It seemed that hunting African Hobbies largely avoided the masses. In the evening, the presence of African Hobbies forced the Swallows to stay at high altitudes where they whirled in dense masses until sunset, and then sped down like an inverted tornado; for African Hobbies, such speeding masses are apparently difficult to attack.

The overall hunting success of 37.9% compares favourably with those of the similar-sized Eurasian Hobby (Table 4), although it should be noted that definitions about what constitutes a hunt differs between studies. The unique setting of a clearing in tropical rainforest at Boje-Ebok may have contributed to the high kill rate, as Swallows forced downhill by Hobbies were "cornered" in the forest edge at the valley bottom. Roosts are normally situated in very open habitats, where Swallows are not hampered by obstacles during ascent or descent (von Vietinghoff-Riesch 1955).

Strategies to reduce predation risks

Many roosts are traditional; some are known to have been in use for over fifty years in a row (Keith *et al*. 1992). They are therefore likely to turn into hotspots for predators that benefit from a predictable food supply. For such locations, predation risk is a fixed property. Barn Swallows seemed to counter the abundance of predators by several strategies, namely safety in numbers, synchronous flying, and – possibly – weight-watching.

Safety in numbers. African Hobbies had highest kill rates when attacking flocks of 2–50 Swallows (Fig. 4), and the risk of predation for an individual Swallow steeply declined with increasing flock size. Anyone having witnessed the mass descent and ditto ascent of Swallows at large roosts recognizes the difficulties of attacking large flocks. The overwhelming majority of Swallows runs a minor risk of predation when part of this rushing mass. In addition, any Hobby having caught a Swallow is one avian predator less on the stage; storing a Swallow, potentially enabling a quick second catch to be made, was not witnessed. Timing of mass arrival and departure was highly predictable, i.e. within a few minutes of sunrise and sunset (see also Rudebeck 1955, Loske 1986). African and Eurasian Hobbies are skilful crepuscular hunters (Keith *et al*. 1992, Pepler 1993, Sergio *et al*. 2001), and it comes as no surprise that at dawn highest success rates were recorded during civil twilight (small numbers of Swallows in the air, in relatively small flocks). The risks of predation are obviously much smaller when departing *en masse* in a short period of time, rather then scattered in small flocks over a longer time interval. A similar strategy was recorded in Guillemot chicks jumping from ledges under conditions of continuous daylight of arctic summer; those jumping during the peak of activity incurred relatively low predation risks (Daan & Tinbergen 1979).

Table 4. Success rates (% of hunts successful, birds and bats only) of European Hobbies (Fsub) and African Hobbies (Fcuv) in various parts of their distribution; observations in England and Hungary were made at Sand Martin colonies, those in Botswana, Ghana and Nigeria at Swallow roosts.

Site, country	Species, status	Nr. hunts	Nr. kills	Success rate	Source
Hampshire, England	*Fsub*, breeding	11	11	100.0	Mead & Pepler 1975
Veluwe, The Netherlands	*Fsub*, breeding	53	28	52.8	Bijlsma 1980
Eastern Germany	*Fsub*, breeding	71	7	9.9	Hantge 1980
Tisza river, Hungary	*Fsub*, breeding	298	15	5.0	Szép & Barta 1992
Chokpak, Kyrgyzstan	*Fsub*, migration	141	12	8.5	Pfander in Sergio *et al.* 2001
Boteti, Botswana	*Fsub*, wintering	12	1	8.3	Bijlsma et al. 1994
Lamto, Ivory Coast	*Fcuv*, breeding	?	?	28.0	Thiollay 1977
Ayensudo, Ghana	*Fcuv*, breeding	4	1	25.0	van den Brink *et al.* 1998
Boje-Ebok, Nigeria	*Fcuv*, breeding	66	25	37.9	this study

Flying behaviour. Swallows heading towards the roost in the evening were flying high and in a leisure mode of flight. Presence of Hobbies over the roost resulted in an immediate increase of flying height and speed of the assembled Swallows, until the birds were almost invisible ("mosquito swarm"). Such flocks were difficult to approach by Hobbies, and few hunts at over 500 m flying height were recorded. The descent of Swallows, apart from being massive and taking place around sunset, was steep and fast. Once the bulk of the Swallows started their descent, there was no stopping. Again, attacking such flocks seems almost impossible. Similarly, in early morning departing birds were always speeding. Even the upward flight was very rapid, and between mass departure and disappearance from sight only few minutes elapsed. Such massed flights were largely ignored by Hobbies, which instead focused on stragglers and small, early or late groups.

Weight-watching. Theoretical models predict that when fat reserves are costly in terms of predation, birds decrease fat reserves in response to high predation risks (McNamara & Houston 1990, Gosler *et al.* 1995). There is evidence from experimental and correlative studies that support this hypothesis (van der Veen 1999, Piersma *et al.* 2003). Swallows in Africa and during migration show large variations in body mass and fat stores in relation to the weather they encounter (Møller 1989, van den Brink *et al.* 2000, Saino *et al.* 2004). During a drought, wintering Swallows in Botswana had low weights and nil fat, whereas years with high rainfall – and hence high availability of insects – resulted in higher weights and fat loads at the same time of year (van den Brink *et al.* 1997). Similarly, the advent of a spell of *Harmattan* in Nigeria in February 2001 coincided with a steep drop in body mass and lack of fat (Table 1: 15.1–15.9 g between 5 and 15 February), with higher weights before and after this spell. Independent of such weather-induced changes, Swallows invariably show an increase in weight (by 2–4 g) and fat load prior to departure to the breeding quarters, normally at the end of the moult cycle (van den Brink *et al.* 1997, van den Brink *et al.* 2000). This indicates that Swallows initiate depositing fat stores just before migration to the north. Whether this is a strategy to reduce the risk of predation at the roost, or to keep energetic costs of flying low (in winter Swallows spend, even while moulting, a considerable part of the day in the air; Keith *et al.* 1992, Cuthill & Houston 1997, van den Brink *et al.* 1997), remains an open question.

Avian versus human predation on roosting Barn Swallows

Estimates of the annual toll taken from roosting Barn Swallows by the local people in the Boje-Enji

region of Nigeria range from 200 000 (Ash 1995, Loske 1996) to 462 000 (R. Yosef & P. Micheloni unpublished). The most factual figure comes from counts of captured Swallows from February through April 1995, when 105 000 Swallows were taken (Ash 1995). The roost is occupied by Swallows from October through March, though in varying numbers. In the course of the winter, numbers apparently built up to a peak in February–March (B. Mkpe pers. comm.). It is likely that in the latter part of the winter, large numbers depart for Europe to be temporarily replaced by newcomers from wintering sites in central and southern Africa. The total number of individuals using the roost may therefore be higher than the maximum estimated at any one time (100 000 to millions; Ash 1995).

Compared with the depredations by man, the impact on Swallow numbers by avian predators is infinitesimal. Probably the most efficient Swallow hunter exploiting the Boje-Ebok roost, the African Hobby, took a maximum daily toll of 14 Barn Swallows (7 African Hobbies, assuming that each catches one Swallow at dawn and dusk). For the individual Hobby this is a significant contribution to its daily energy requirements, as two Swallows cover about 50–60% of daily food consumption (estimated at approximately 25% of its body weight: Kirkwood 1981, Newgrain *et al.* 1993). The daily capture of 14 Swallows during the six months of their presence only amounts to an annual toll of some 2500 Swallows, and a crude estimate of predation indicates that the combined raptor guild may take twice that number. The omnipresence of avian predators at Swallow roosts is therefore unlikely to impact prey numbers (see also Newton 1998), but probably is an important asset in the evolution of behaviour.

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SAMENVATTING

Boerenzwaluwen *Hirundo rustica* gebruiken in Afrika gemeenschappelijke slaapplaatsen, variërend in omvang van honderden tot ettelijke miljoenen vogels. Veel van deze slaapplaatsen zijn traditioneel en soms decennia achtereen in gebruik. Ze vormen een aanlokkelijke voed-

selbonanza voor roofvijanden, die immers op gezette tijden een tafeltje-dek-je voorgeschoteld krijgen. Alle slaapplaatsen die wij in Botswana, Ghana en Nigeria bezochten, werden door een verscheidenheid aan roofvogels (en uilen) geëxploiteerd. De slaapplaats in Nigeria was een geval apart, namelijk gelegen in olifantsgras op een berghelling temidden van tropisch regenwoud. De Boerenzwaluwen arriveren 's avonds laat op de slaapplaats, gemiddeld zo'n 20 min voor zonsondergang. Ze zwermen vervolgens hoog in de lucht totdat de zon ondergaat; in krap 10 min suizen de honderdduizenden zwaluwen dan als een omgekeerde tornado naar beneden, een duizelingwekkend schouwspel. 's Ochtends vroeg vertrekken de eerste zwaluwen 0–9 min voor zonsopkomst, eerst in kleine groepen, gevolgd door 90% van de massa kort na zonsopkomst. Hun vlucht is razendsnel, laag de contouren van de vegetatie volgend (vaak gedwongen door activiteiten van roofvogels) of steil omhoog in krappe spiralen. In beide schemerperiodes zijn de zwaluwen slechts 20–40 min in de lucht boven de slaapplaats, een krap venster voor gevleugelde predatoren om in te jagen. Niettemin waren Afrikaanse Boomvalken *Falco cuvieri* zeer succesvol in hun jacht. De valken anticipeerden op komst en vertrek van de zwaluwen door 2–14 min eerder boven de slaapplaats aanwezig te zijn. Vlieghoogte, jaagwijze noch tijdstip ten opzichte van zonsopgang of zonsondergang waren van invloed op het succes waarmee zwaluwen werden gevangen. Hun jachtsucces leek daarentegen afhankelijk te zijn van de groepsgrootte van zwaluwen. De valken waren het meest succesvol met het bestoken van groepjes van 2–50 zwaluwen; jacht op eenlingen en grotere groepen was minder geslaagd. Gemiddeld was 38% van de jachtvluchten raak. Per schemerperiode waren vermoedelijk alle Afrikaanse Boomvalken in staat hun zwaluw te vangen. Meer dan één zwaluw vangen was onmogelijk, omdat daarvoor de tijd ontoereikend was (bedenk dat jacht tijdens de 10 min van massavertrek en -inval erg moeilijk was) en er geen aanwijzingen waren dat de valken er een voorraadkamer op na hielden (wat ze in theorie in staat kan stellen meer dan één zwaluw te pakken).

De strategie van Boerenzwaluwen om in grote groepen te slapen, aankomst en vertrek grotendeels in de schemering te laten plaatsvinden, hun aanwezigheid boven de slaapplaats te beperken tot uiterlijk een half uur, massaal in te vallen en op te stijgen en pas op te vetten aan het eind van de ruicyclus (vlak voor vertrek naar de broedgebieden) bemoeilijkt de jacht van gevleugelde predatoren behoorlijk. Niettemin waren Afrikaanse Boomvalken op hun manier ook buitengewoon succesvol. Door tijdig aanwezig te zijn, vooral te jagen op kleine groepjes en gebruik te maken van de specifieke terreingesteldheid (open plek temidden van regenwoud, waardoor laag vertrekkende zwaluwen tegen de bosrand konden worden opgejaagd) waren vermoedelijk alle valken elke schemerperiode verzekerd van de vangst van één zwaluw. Zodoende beliep de totale vangst van de zeven aanwezige Afrikaanse Boomvalken gedurende de zes maanden van aanwezigheid van de zwaluwen naar schatting hooguit 2500 vogels, een peulenschil in vergelijking met de minimaal 100.000 zwaluwen die de lokale bevolking op ingenieuze wijze jaarlijks voor de pot vangt.

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