Aerial Hunting Techniques and Predation Success of Hobbies Falco subbuteo on Sand Martin Riparia riparia at Breeding Colonies

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Aerial hunting techniques and predation success of Hobbies *Falco subbuteo* on Sand Martin *Riparia riparia* at breeding colonies

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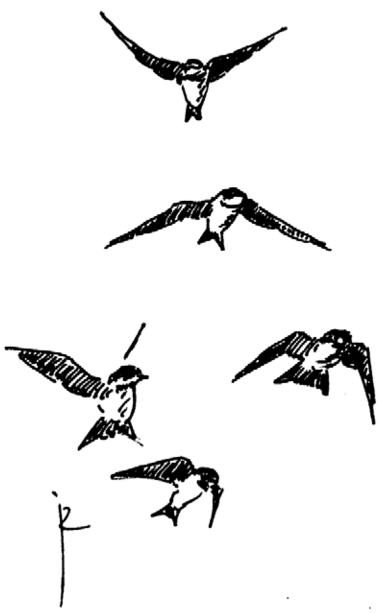
We analysed 291 attacks by 15 male Hobbies *Falco subbuteo* at 13 different Sand Martin *Riparia riparia* colonies in Austria, Hungary, and Serbia in 2004 and 2005. We predicted that the choice of escape strategy would be context-dependent and related to the condition and age of swallows and relative position and flight characteristics of both predator and prey. We predicted that swallows would be unable to escape falcons in a level chase and would not seek cover. We predicted that falcons would be more successful when juveniles were present. Hunting success rates were higher during the swallows' post-fledging period, probably because of the weaker flight performance of juveniles. Invariably, adult swallows tried to outclimb falcons, while probable juveniles also tried to escape to cover. Hobbies most often attacked adult swallows by a fast approach from great heights and distances. In contrast, in the post-fledging period, when juveniles were available, low horizontal attacks and long climbing chases were common. In doing so, Hobbies at times prevented juvenile swallows from taking cover and were, in turn, sometimes able to outclimb and capture them. Significantly more attacks were abandoned during the post-fledging period. Sand Martins were unable to escape Hobbies in a level chase. Individual male Hobbies showed no difference in hunting success, maybe because all were experienced. The number of Sand Martins present at the time of attack did not influence hunting success. The results are discussed in the light of the anti-predator strategies of animals living in groups.



Key words: Hobby, Sand Martin, prey phenology, living in groups, hunting and escape techniques, predation success

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Among the important factors driving group formation in animals are potential anti-predator benefits, including the many-eyes effect, predator confusion, the dilution of individual risk of being caught when part of a large group, and the selfish herd effect (Krause & Ruxton 2002). The many-eyes effect postulates that an increased number of potential prey individuals scanning for predators are more effective at detecting their approach, and this early detection is associated with the transmission of this information throughout the group (Kenward 1978, Godin *et al.* 1988, Cresswell 1994). Groups can act to confuse predators, and so when faced with larger groups, predators have a lowered hunting success because they are unable to single out an individual on which to concentrate their attack (Neill & Cullen 1974, Caraco *et al.* 1980, Krakauer 1995, Carere *et al.* 2009). The dilution effect predicts the likelihood of any individual of a group being caught by a predator is reduced as group size grows (Foster & Treherne 1981, Godin 1986, Zoratto *et al.* 2010). Hamilton (1971) argued that individuals on their own are more vulnerable to predators, as a flock member gains protection from the vulnerability of those around it (selfish herd theory; cf. Morton *et al.* 1994).

In addition to these potential group benefits, there are also costs of grouping (Krause & Ruxton 2002). Examples of potential costs that might influence individual vulnerability include the possibility that predators might be attracted by large prey aggregations, that group members are not identical (e.g. age or sex differences), and that predators have the ability to adapt their hunting technique (Landeau & Terborgh 1986, Hilton *et al.* 1999, Quinn & Cresswell 2004). Studying the costs and benefits of group formation is essential for understanding the evolution of the anti-predator behaviour of animals living in groups (Krause & Ruxton 2002). Empirical data are important to model the prey–predator "evolutionary arms race" and collective behaviour (Lima 1993, Sih & Christensen 2001, Lima 2002, Lingle *et al.* 2008).

We described the techniques used by male Hobbies *Falco subbuteo* hunting Sand Martins *Riparia riparia*, and analysed hunting success rate in relation to prey flock size. Sand Martins nest colonially and are regular prey of Hobbies during the breeding season (Mead & Pepler 1975, Szép & Barta 1992). However, no detailed analysis of the interaction between Sand Martins and Hobbies has been undertaken. We expected that swallows choose escape strategies depending on their state (e.g. physical condition related to age), or their position and speed relative to the predator (Hedenström & Rosén 2001). Furthermore, we expected that the hunting success rates of Hobbies are higher during the time when juvenile swallows are available, as juveniles are weaker flyers than adults. The results are discussed in the light of potential anti-predator strategies of animals living in groups.

METHODS

Species and study sites

The Hobby is a small, migratory falcon that breeds throughout the Palaearctic. It typically rears two or three young, which fledge around early August. The Hobby is renowned for its aerial hunting skills, taking small birds and insects singly in mid-air, often after a long dive or chase. Typical avian prey includes swifts, swallows, starlings, larks and sparrows (Bijlsma 1980, Fiuczynski 1987, Chapman 1999).

Sand Martins breed in colonies that sometimes include several thousands of pairs. Swallows nest in sandy banks along rivers, but also use sandy walls created in sand pits and quarries. They typically lay four to seven eggs and raise one or two broods per season. On the summer breeding grounds, swallows hunt small insects, usually within 1 km of their colony (Cramp 1988).

Observations were made at 10 sandpits in eastern Austria from April to August 2004 (centred on about 48°00'N, 16°35'E), at one large colony along the river Tisza in Hungary in July 2004 (48°11'N, 21°28'E), and at two big colonies along the Danube in Serbia in July 2005 (44°49'N, 21°20'E). Observations in Austria covered the whole Sand Martin breeding season while those in Hungary and Serbia were confined to the post-fledging period. Observation bouts lasted one hour and sandpits in Austria were randomly chosen. The Austrian study area was dominated by intensive agriculture, and colony sizes ranged from about 10 to 300 individuals. The Hungarian and the Serbian colonies were situated in large riverbanks, and each held up to about 2000 swallows.

Hunting and escape behaviour

Direct observations of Hobby attacks at Sand Martin colonies were taken spanning all daylight hours. We recorded all attacks, but analysed only those made by males because females rarely hunt on their own (Fiuczynski 1987) and cooperation between partners and differences in agility between the sexes might confound the results (Chapman 1999, Krüger 2005). In the rare cases when two male Hobbies hunted at the same colony, we identified individual falcons by their flight paths (to and from their nesting areas) and plumage. In those cases male Hobbies typically interacted aggressively, and no attacks on swallows occurred. As the study colonies were separated by at least 10 km and Hobbies have a hunting range of about 6 km (Chapman 1999), we assumed that the majority of the males we observed at different colonies were not the same individuals.

The initiation of an attack by a falcon was characterized by either fast direct powered flight (high-frequency, deep wing beats) or, rarely, a stoop (folded wings from high altitudes). Two types of attacks were observed: one where the falcon followed through on its attack on a flock or individual (non-abandoned attack), and one where the falcon aborted the attack before reaching the flock or individual (abandoned attack) (cf. Dekker 2003 for the Peregrine Falcon *Falco peregrinus*). In the case of non-abandoned attacks, Hobbies made

1–20 dives at the targeted swallow. If falcons attacked different swallows during a hunting bout we considered each attack and separated the data.

For each attack, the total number of Sand Martins in the air was recorded, as was their escape reaction (turning gambit, climbing, taking cover, or combinations thereof), the hunting technique of the falcon (dive, horizontal chase – about 10 degrees above and below horizontal –, and climb), and whether the attack was successful. Colonies were typically situated in open landscapes, and most attacks were made near the centre of the colony. Therefore, the success of a hunt could be determined easily because attacks usually occurred at close range, and captured Sand Martins are sufficiently large to be seen in the Hobbies' talons. A hunting flight was considered successful if the falcon caught and killed the swallow.

In addition, the number of Sand Martins in the air was recorded every half hour and counts were made when numbers of Sand Martins in the air appeared to change greatly. At small colonies, it was possible to count swallows in flight; at large colonies the mean count estimates of at least two experienced observers was recorded. Observations were conducted from a distance of about 100–200 m, using 10×40 binoculars (Szép & Barta 1992).

After a catch, the Hobbies typically carried the prey out of sight, and therefore, age of prey normally could not be determined. Only recent fledglings were recognized in the field by their weaker flight and more rounded wingtips; they are still fed by adults and, at close range, pale fringes of feathers are visible on the upperparts. Nevertheless, it is reasonable to assume that juveniles were hunted and caught as soon as available because juveniles of any avian prey species are a major component of the Hobbies' diet (see Fig. 73; Bijlsma 1980). Sand Martins fledge from mid-June onwards (Szép & Barta 1992), and this was confirmed for the colonies we studied (Probst & Tucacov, unpubl. data).

Data analysis

We used the χ^2-test, G-test and Fisher's exact test to determine significance ($P \leq 0.05$) of our results. A Generalized Linear Mixed Model (GLMM) with a binomial error distribution was calculated to test for a correlation between attack outcome and numbers of Sand Martins in the air during an attack. Thereby, the attack outcome (coded as 0 = no success, 1 = successful) was regressed against the square-root transformed number of Sand Martins and, to minimize the effects of non-independent observations, individual predator identity was included as a random factor. This was calculated using data from males only where ≥7 hunts were observed. The GLMM was carried out using the program R (R Development Core Team 2007).

RESULTS

A minimum of 10 male Hobbies in Austria, one in Hungary and four in Serbia were seen hunting at the 13 study colonies. Only one falcon was identified per colony in Austria and Hungary, while at both colonies in Serbia two Hobbies were present. Of the 296 attacks recorded, the outcome was known for 291 (98.3%), and we used these in our analyses. We pooled data from the post-fledging period after mid-June, as hunting success rates (percentage of attacks successful) did not differ between Austria (12.75%), Hungary (11.3%) and Serbia (14.46%), regardless of whether we included ($\chi^2_2 = 0.39$, $P = 0.82$) or excluded (17.81%, 15.4%, 21.82%, $\chi^2_2 = 1.21$, $P = 0.55$) abandoned attacks. Hunting success was not different (marginally) between pre-fledging (3.8%) and post fledging (13%) periods when we included abandoned attacks (2/51 vs. 31/207, $\chi^2_1 = 3.7$, $P = 0.054$). However, if these were not included, Hobbies were significantly less successful during the pre-fledging period (4%) than during the post-fledging period (18.6%) (2/48 vs. 31/136, $\chi^2_1 = 6.3$, $P = 0.025$).

In the pre-fledging period, Sand Martins invariably tried to outclimb Hobbies and never fled towards cover (Fig. 1). During the post-fledging period, many swallows tried to escape by gaining altitude, but 16.8% sought cover to escape, which was significantly different from the pre-fledging period (Fisher's exact $P < 0.001$). During the post-fledging period, four (13%) of the 31 Sand Martins were caught in cover. These included two in forested areas, and once each in sunflower and grain fields. Attacks were abandoned more often during the post-fledging period (5.7% vs. 29.8%, $\chi^2_1 = 13.36$, $P = 0.001$).

Hobby hunting techniques were recorded for non-abandoned attacks in Austria ($n = 119$) (Fig. 2). A comparison between the pre- and post-fledging periods revealed that attacking Hobbies made significantly more climbs for their prey after mid-June (2% vs. 22.9%; $G = 12.6$, $P = 0.01$). 23% of captures in Austria in the post-fledging period resulted after climbing flights. Such climbs could last for over 5 min.

Hunting success in the post-fledging period was not associated with the number of Sand Martins in the air (Fig. 3), neither when abandoned attacks were included

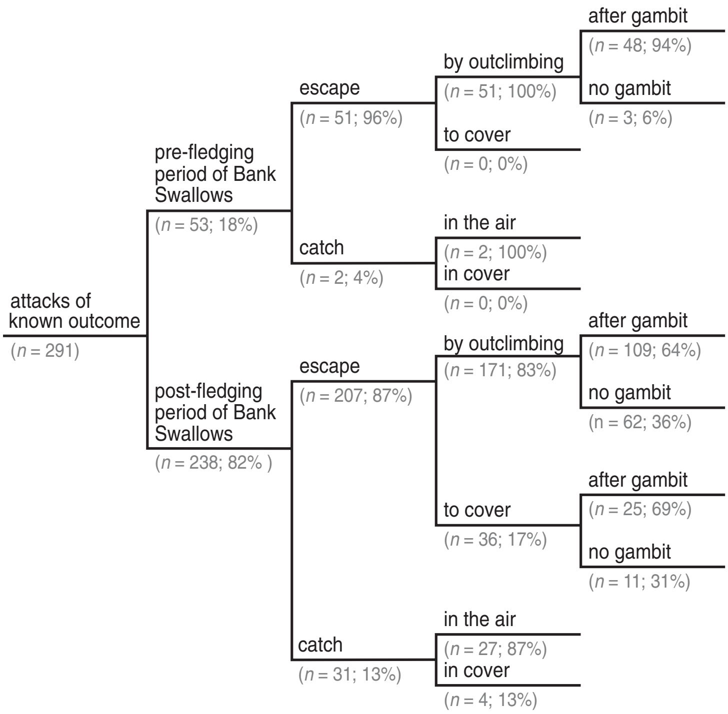

Figure 1. Outcome of attacks by male Hobbies (observations in Austria, Hungary and Serbia; n = 291).

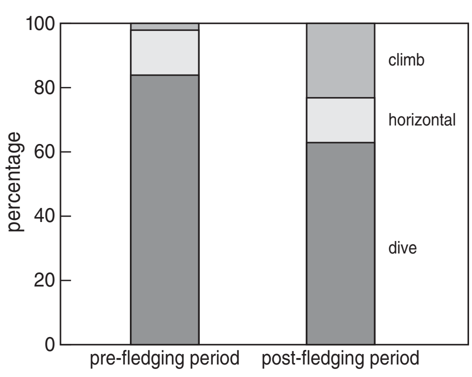

Figure 2. Hobby hunting techniques during the pre-fledging (before mid-June) and post-fledging periods of Sand Martins (observations in Austria; n = 119).

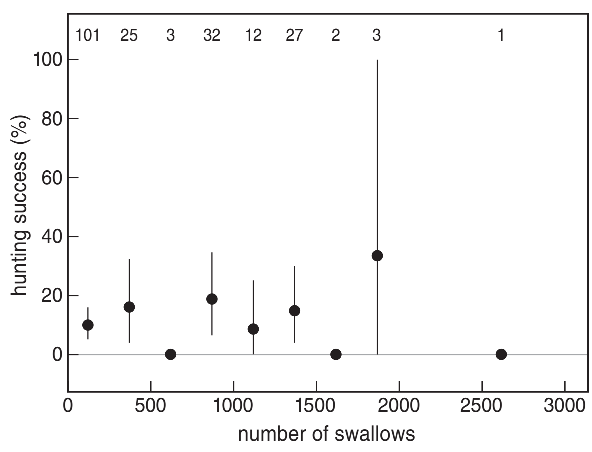

Figure 3. Hobby hunting success during the post-fledging period in relation to the number of Sand Martins present (by 250-individuals categories). Means with 95%-confidence intervals and sample sizes (based on all attacks) are indicated.

(n = 206; P = 0.57) nor when they were excluded (n = 141; P = 0.35). The same held true when estimating quadratic effects (P = 0.72 and P = 0.51, respectively), controlling for a potential bi-directional influence of swallow numbers on hunting success (cf. Bijlsma & van den Brink 2005). The inter-individual variance (random factor) caused by male Hobbies was estimated to be close to zero (Table 1).

DISCUSSION

In this investigation we studied the aerial hunting techniques and predation success of Hobbies on Sand Martins at breeding colonies. We found that escape performance differed in the pre- and post-fledging period (Fig. 1; cf. Cooper 2006), and this corresponded to different hunting tactics by falcons to a certain extent (Fig. 2). Adult swallows are extraordinarily good flyers in open areas but cannot manoeuvre well in vegetation. Given that Hobbies started with an advantage in initial height and speed, the first stage of escape by adult swallows was to flee in level flight (cf. Cramp 1988), however, as soon as the falcon had reached the intended swallow and dived on it, adult swallows consistently tried to outclimb Hobbies. Our results suggest that once a targeted adult has attained a certain altitudinal advantage it will not be caught. If the falcons' initial position was lower than the adult swallow, the target invariably attempted to escape by climbing. Other studies ($n > 500$ attacks) have confirmed this latter finding for adults in other species of mid-air foragers, like Common Swift *Apus apus*, Barn Swallow *Hirundo rustica*, and the House Martin *Delichon urbicum* and probably Skylarks *Alauda arvensis* (cf. Probst 2006), while other songbirds such as finches, buntings and wagtails try to outmanoeuvre falcons and reach cover (Probst, unpubl. data). In order to overcome this disadvantage Hobbies most often attacked adult Sand Martins from a fast, shallow, powered stoop initiated from a great distance and height.

However, when hunting juveniles, that are not as strong as adults and unlike adults would sometimes flee toward cover, Hobbies more often attacked in low, fast, level flight to cut them off from cover to chase them subsequently in a climb. We hypothesize that with increasing age swallows are more capable of escape (by climbing) because they gain experience and their flight feathers and muscles are more developed. By using additional escape tactics to those used by adults, juveniles can reduce the falcons' hunting success. In line with our expectations, differences in physical condition between adults and juveniles, the relative position of prey and predator, and the speed and direction of prey and predator influenced hunting and escape strategies. As a consequence, abandoned attacks were much more common when juveniles were available, because they sometimes reached cover, and because at some point after fledging they were as physically capable of escape after long climb chases.

Reported hunting success rates vary widely for the Hobby (Bijlsma 1980, 39–63%; Hantge 1980, 10%; Szép & Barta 1992, 4–16%; this study, 3.8–18.6%) as for the related but larger Peregrine Falcon *Falco peregrinus* (Jenkins 2000, Zoratto *et al.* 2010; 9–84%). Although reasons for this variation are poorly understood, it seems that factors such as prey type (Dekker & Taylor 2005), prey vulnerability (Cresswell & Quinn 2004), hunting technique (Bijlsma 1980, Hedenström & Rosén 2001, Roth & Lima 2003), predator experience (Dekker & Taylor 2005), cooperative hunting (Bednarz 1988, Ellis *et al.* 1993), or sample size effects (Page & Whitacre 1975, Dekker 1988) are contributory. In this study, the hunting success rates of male Hobbies attacking Sand Martin colonies were primarily associated with whether attacks were made before or after swallow fledging; hunting success post-fledging was about three to five times higher than during the pre-fledging period. Although we were unable to directly record the exact proportion of juveniles that were hunted during the post-fledging period, we have no explanation for the higher hunting success other than the presence of juveniles, especially as there is no indication of changing flight abilities in adults between periods before and after fledging (Cramp 1988; pers. obs.). Adults should be, in fact, more vulnerable during the pre-fledging period, since they display, dig nesting holes and feed young during that time (cf. Sirot & Touzalin 2009). Further, Bijlsma (1980) reports that pluckings found under Hobby nests show that many juvenile swallows are preyed upon, and that Hobbies hunt alternative avian prey more often before the fledging of swallows and swifts. Indeed, we did observe eight successful captures of just fledged rounded-winged Sand Martin juveniles and we identified the remains of one juvenile immediately after a Hobby killed it. If our assumption that the swallows outclimbed by Hobbies were all juveniles is true and we add to this the nine definite cases

Table 1. Percentage of successful attacks during the post-fledging period for each individual male Hobby, separately for non-abandoned and all attacks.

Hobby	Non-abandoned attacks		All attacks	
	% success	*n*	% success	*n*
1	18.2	11	18.2	11
2	15.4	13	11.1	18
3	12.8	39	10.9	46
4	14.3	7	7.1	14
5	16.2	37	11.8	51
6	29.4	34	16.9	59
7	-	0	0.0	7

in which juveniles were captured, then a minimum of 55% of captures during the post fledging period would have been of juveniles. However, although it is intuitively appealing to think that young and inexperienced prey should be preferentially attacked, this has been proven in relatively few taxa. Examples for avian predators are Goshawk *Accipiter gentilis* (Tornberg 1997) and large falcons (*Falco peregrinus, F. pelegrinoides, F. biarmicus*; Bijlsma 1990, Cade & Burnham 2003, Dekker & Taylor 2005).

Hunting success was not different among the individual falcons. This might be because, as Hobby males do not breed before their third calendar year, all males are experienced and have a full repertoire of hunting techniques, and because the landscape was very open, limiting individually different hunting tactics. Interestingly, hunting success was independent of the number of potential prey present in the air, although many theories predict larger flocks to be safer during an attack (Krause & Ruxton 2002; but see Lindström 1989; cf. Bijlsma & van den Brink 2005). Foremost, potential benefits of grouping are thought to arise from the many-eyes effect (Vine 1971, Pulliam 1973, Ebensberger *et al.* 2006) and from predator confusion (Neill & Cullen 1974, Krakauer 1995). We speculate that Hobbies may at least partially overcome Sand Martin vigilance by attacking at high speeds. Published values for Hobby flight speeds suggest that they could arrive at the colony travelling two to three times as fast as Swallows can fly in horizontal flight (Bijlsma 1980, Glutz von Blotzheim & Bauer 1985). Concerning the idea that groups increase predator confusion, swallows do not fulfil important predictions of the theoretical model proposed by Krakauer (1995). Firstly, Krakauer (1995) states that increased protection occurs following group compaction, and this has been shown from field studies (e.g. Carere *et al.* 2009). Sand Martins, however, forage in very loose groups dispersed around the colonies, which typically do not compact during falcon attacks (cf. Sirot & Touzalin 2009). According to our data, falcons most often (>90%) concentrated their attacks on single swallows and did not need to initially disperse a concentrated, coordinated flock. Secondly, Krakauer (1995) stated that the confusion effect is most effective when all individuals are alike. During pre-fledging, falcons always attacked swallows at the trailing end of the flock (cf. Michaelsen & Byrkjedal 2002), while during the post-fledging period they sometimes by-passed a number of swallows to attack another individual. This observation reinforces the idea that Hobbies hunt non-randomly in the post-fledging period, when they were most likely to attack slow and inexperienced juveniles.

The observation that attack success was independent of the number of Sand Martins present implies that the per capita risk of predation during an attack declined proportionally with colony size (Foster & Treherne 1981). However, further studies on group size dependent properties are necessary as not only the dilution effect but also the encounter rate has to be taken into account when assessing the real threat to a potential prey individual living in a colony (Wrona & Dixon 1991).

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SAMENVATTING

Een belangrijk voordeel van het leven in een groep is de kleinere kans om ten prooi te vallen aan predatoren. Er zijn talloze theorieën ontwikkeld hoe dit voordeel tot stand zou kunnen komen. Zo zou de kans om een naderende predator te ontdekken toenemen wanneer meer individuen samen optrekken, of de predatoren zouden in verwarring raken door de talrijkheid van hun prooien. Om dergelijke theorieën te testen en ontwikkelen zijn veldwaarnemingen nodig. In dit onderzoek is geanalyseerd hoe mannetjes van de Boomvalk *Falco subbuteo* Oeverzwaluwen *Riparia riparia* vangen. Bij 13 zwaluwkolonies in Oostenrijk, Hongarije en Servië werden 291 aanvallen door Boomvalken geregistreerd. Volwassen zwaluwen probeerden aan de Boomvalken te ontkomen door snel hoogte te winnen, en dat lukte in 96% van de aanvallen. Vanaf het moment dat de jonge

zwaluwen uitvlogen nam het succes van de Boomvalken toe, en nog maar 87% van de zwaluwen wist aan de aanvaller te ontkomen. Jonge vogels ontsnapten vaak door dekking in begroeiing te zoeken, wat overigens niet altijd lukte. Jonge vogels die probeerden hoogte te winnen bij nadering van een valk ontbrak het kennelijk aan kracht en snelheid om te ontkomen en de waarnemingen duiden erop dat vooral deze vogels slachtoffer werden. Tegen de verwachting in had het aantal rondvliegende zwaluwen geen effect op de kans van een succesvolle jacht door Boomvalken. (KvO)

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