

Is “banging” an antipredator behavior in Common Swift (*Apus apus*)?

Grzegorz Oloś

Chair of Biotechnology and Molecular Biology, Faculty of Natural Science and Technology, Opole University, Kominka Street 6, 45-032 Opole, Poland. E-mail: golos@uni.opole.pl

Received 5 July 2016, accepted 10 January 2017

Prey species show various types of antipredator behaviors to avoid predator attacks. Common Swifts (*Apus apus*) show specific behaviour where birds make almost a full stop during flight – this is referred to as “banging” behavior. This behaviour may be directed towards a conspecifics which, for example, enters a nesting or a roosting site, or clings to a wall of a building. The bird showing this behavior is usually accompanied by conspecifics, which also copy its flight pattern. Actual explanations for this behavior are often inconsistent and unclear. This study has reconsidered such explanations and focused on the novel role of this behaviour as a potential antipredatory adaptation against the Common Kestrel (*Falco tinnunculus*). Observations of Common Swift behaviour were carried out in May–September 2014 and May–August 2015 in Opole, SW Poland, giving 1,367 observations of nesting/roosting activities, 868 observations of “banging” behavior and 37 attacks of kestrels on swifts. There was a negative correlation between the number of successful hunting attempts and the number of Common Swifts showing banging behaviour. The study covers different aspects of banging behavior and major factors correlating with its occurrence.



1. Introduction

The Common Swift (*Apus apus*) lives and nests in colonies and hence it has developed social behaviors (Cutcliffe 1951, Lack 1956, Rothgänger and Rothgänger 1973, Tiggés 1999). One of such behaviours, specific to Common Swifts, is called “banging” behaviour. Banging behaviour may occur whenever a Common Swift clings against the wall, enters a nesting/roosting place, or when it skims a random place like wall or roof. A conspecific making a clear immediate flight stop following the first one is called a “banger”. If it glides closely instead of making a flight stop, this behavior is called “skimming” behavior. Banging be-

havior has been reported since the beginning of Common Swift studies at Oxford Tower colony in London (Lack & Lack 1952, Lack 1956) and in the tower of Saints Philip and James Church, Ilfracombe (Cutcliffe 1951, 1955). Multiple explanations have been proposed for such behaviour, including yearlings returning to their home nests (Cutcliffe 1955, Lack 1956, Kaiser 1992), immature non-breeders checking potential nesting and roosting places (Lack 1956, Farina 1980, 1988, Kaiser 1997), or showing the nesting space (Vleugel 1952). Alternatively it has been proposed as a way of “colony controlling” (Farina 1980, Tiggés 1995) or being an aspect of aggressive, territorial behavior (Lack 1956, Roper 1960, Kaiser 1992,

1997). The aim of this study was to explore the causes of this behavior, to discuss current explanations, and to study whether its occurrence is associated with predation risk events.

2. Material and methods

2.1. Study area

Research was conducted at AK Estate in Opole (50.679° N, 17.940° E) in southwestern Poland (later referred to as AK Estate colony). Nesting/roosting places of Common Swifts were located in 3–11 floor blocks of flats and 2–3 floor serial buildings of six neighbour blocks. Nesting/roosting places were located in the thin gaps underneath the rooftops, window sills, in ventilation openings, sometimes in Styrofoam insulation layer holes and in old Common House Martin (*Delichon urbica*) nests. The height of the nesting/roosting places ranged 5–25 meters. At least two pairs of Common Kestrel (*Falco tinnunculus*) bred inside the observed AK Estate colony, and were seen hunting for swifts. That predator was also found at other observed colonies. Additional observations were conducted at Common Swift colonies in Opole city, Niemodlin city, and Strzelce Opolskie city (Opole Province, suburban and old industrial areas, southwestern Poland), as well as in Katowice and Wrocław agglomerations (southwestern Poland), to verify the occurrence of this behaviour across nesting sites.

2.2. Field methods

Based on the daily activity schedule of the Common Swifts (Farina 1988, Tigges 1999) and according to own observations, the morning 6:30–10:30 am, midday 12:00–1:00 pm, and evening (a half of an hour before and after sunset) were considered the best time for observations. Data was collected by naked-eye observations supported with a still camera. Observations were made without entering the rooftops or marking the individuals, which could distract the breeding individuals (Lack 1956, Farina 1988). Each event involving at last one bird entering the hole in the building wall

or clinging at wall was considered as a nesting/roosting activity event. Next, response time, i.e. time to banging (in seconds) was measured after a single nesting/roosting activity was observed until banging behaviour occurred in that location. If no banging behaviour was observed within 10 seconds, the event was considered not to include banging behaviour. If one Common Swift was found clinging to the wall, its conspecifics were observed to be provoked to show banging behaviour. The same observations were made by Farina (1980).

In most cases banging behavior ended when the first bird, which undertook the nesting/roosting activity, entered a nest or flew away. Birds participating in screaming parties were tracked, and it was found that some of them showed banging behaviour just after returning from screaming parties. To avoid pseudoreplication, during each observation period the observer moved along the colony spending a maximum of 10 minutes around one of six blocks, randomly chosen, inside the colony. Whenever banging was observed toward the same nesting/roosting place (e.g., hole underneath the window still), the average values were used in the analysis. The data points are relative frequencies of nesting/roosting activity with banging made by Swifts during one observation period (about = 0.5 to 1 hour).

The total number of Swift individuals flying inside the colony was measured at the beginning of each observation (around a single block of flats) by counting the flying individuals in area specified as not further than 100 m in the altitude level and 25 m vertically from the location of the observed nests. Each observation gave at least six datapoints of the number of flying Swifts, from which an average was taken.

Observations were carried out from the beginning of May till the departure of the local population, 1–3 days per week and three times a day if possible. Age (adult/immature) and colony affiliation (affiliated/not affiliated) of observed birds were based on breeding status, nests location by nestlings calls, and participation in screaming parties (only members of the colony participate in screaming parties, Lack 1956, Rothgänger & Rothgänger 1973, Farina 1988, Henningsson *et al.* 2010).

2.3. Banging behavior

This study focused on banging/skimming (called banging behavior later in the text) behavior, which is an interaction between two or more Common Swift individuals. The first observed bird may undertake different nesting/roosting activities like entering a nesting/roosting place or making a flight stop there. Any of the conspecifics of the same colony that makes a flight stop or clings at the same place just after (not later than 10 seconds, see above) the first bird, or a conspecific that flies very close to the first bird (at a distance of a quarter of a meter or less) is a “banger”. Often many birds presented banging behavior simultaneously towards one of the conspecifics or location. Banging always interferes with normal flight, by slowing down rapidly, by hovering for about a second, or by hanging to a wall close to the place where a conspecific was before. Banging behaviour was never observed among birds flying out of the nesting/roosting site. In many cases banging behaviour ended with physical contact between the birds. This included skimming with wings, banging on each other, pecking, grabbing with legs, and pulling out of the nesting/roosting place. If a bird was pulled out, no further aggressiveness was shown against it. Physical contact occurred especially in three cases: 1) towards the birds that were clinging against a wall, 2) towards those individuals which did not stop to enter the nesting/roosting place after banging behaviour without physical contact, and 3) towards those individual which were not totally hidden in their nesting/roosting places, with a fragment of their body protruding. Banging behavior appears exclusive to this species.

2.4. Statistical analysis

Correlation between different aspects of banging behaviour (time of day, timing of breeding (month), number of birds flying in the colony) during observation periods were calculated using two-tailed test of Spearman correlation coefficient (r_s) due to its invulnerability to the outlier results and in case of lack of normal distribution for the measured values. Differences between relative frequencies of nesting/roosting activities with banging, in relation to timing of breeding (month)

and time of day were analysed with Kruskal-Wallis ANOVA test. The null hypothesis were that none of the variables influences the relative frequencies of banging behaviour and frequency of banging behavior does not influence the success and number of hunt attempts by Common Kestrel.

3. Results

3.1. Frequency of banging behavior

Banging behavior was documented in all the observed colonies. During the entire study 1,367 nesting/roosting activities were observed, and of them 868 included banging behavior (i.e., 63.49%) at AK Estate colony. Three factors positively correlated with the occurrence of banging behavior: 1) the total number of Common Swift individuals flying inside the colony, 2) timing of breeding during the breeding season (month) and, 3) the time of day. A strong positive correlation between the total number of Common Swift individuals flying inside the colony and the relative frequencies of nesting/roosting activities with banging was found in the month of July 2014 ($r_s = 0.687$, $N = 33$, $p < 0.001$), and it was found to be very strong in July 2015 ($r_s = 0.87$, $N = 34$, $p < 0.001$) (Fig. 1).

Relative frequencies of nesting/roosting activities with banging behaviour during the two studied seasons depended on the timing of breeding during the breeding season (Kruskal-Wallis test: for 2014, $H = 40.75$, $df = 4$, $p < 0.001$ and for 2015, $H = 37.71$, $df = 4$, $p < 0.001$), and it reached its climax in the month of July in both years (Fig. 2).

The averages of relative frequencies of banging behaviour in July 2014 and 2015 during different times of the day (morning, noon, and evening, respectively), were 0.628 (SD = 0.134), 0.487 (SD = 0.16), 0.945 (SD = 0.08) ($N = 33$) and 0.671 (SD = 0.154), 0.502 (SD = 0.142), 0.893 (SD = 0.105) ($N = 34$), respectively; and they were significantly different (Kruskal-Wallis test for the year 2014, $H = 20.81$, $df = 2$, $p < 0.001$ and for 2015, $H = 15.73$, $df = 2$, $p < 0.001$).

3.2. Number of birds showing banging behavior per nesting/roosting activity

The number of birds showing banging behavior per single nesting/roosting activity varied, reach-

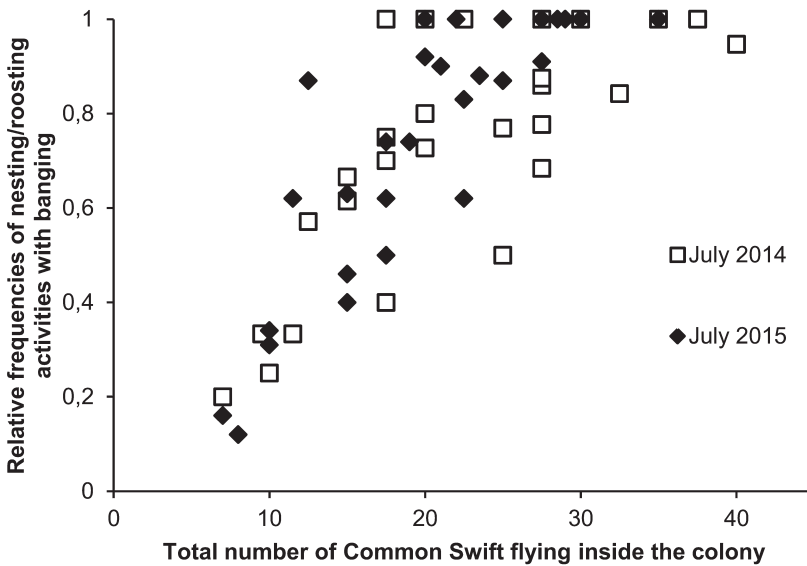


Fig. 1. Total number of Common Swift individuals flying inside the colony and the relative frequencies of nesting/roosting activities with banging behaviour at AK Estate colony during July 2014 and 2015.

ing its maximum in July. While excluding the nesting/roosting activities without banging, the weighted mean for the number of birds showing banging behavior per single nesting/roosting activity in July of 2014 and 2015 combined was 2.25 (SD = 1.69) ($N=474$ events of banging behavior).

3.3. Response time from nesting/roosting activity to banging

The average time of the first banging bird to occur after a nesting/roosting activity was less than two seconds for each month of the study. Often, a group of birds was found to make the banging at an exact same time. In July 2014 and in July 2015, the banging occurred in less than one second in 73% and 78% of cases, respectively ($N = 474$).

3.4. Predation

Common Kestrels mostly used the sit-and-observe technique and were found to attack the swifts during their entry to the nesting/roosting sites by surprise. Of the 37 attacks documented, the success of the attack was determined for 33. Only one chase in open air was successful during the two years of observations. There was a very strong, negative correlation between the number of Common Kestrels hunt attempts and the number of banging

Common Swifts per nesting/roosting activity ($r_s = -0.94, N = 33, p < 0.001$). Similar correlation was found between the number of successful Common Kestrel hunt attempts and the number of banging Common Swifts before attack ($r_s = -0.87, N = 33, p < 0.01$) (Fig. 3).

4. Discussion

In the literature, various explanations for banging behaviour have been suggested (Vleugel 1952, Cutcliffe 1955, Lack 1956, Farina 1980, Bretagnolle 1993, Tigges 1995, Tigges & Mendels-

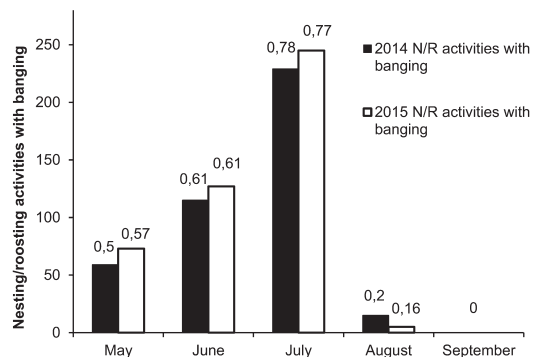


Fig. 2. Proportion of nesting/roosting activities with banging behaviour at AK Estate colony in 2014–2015. Relative frequencies are given above the columns.

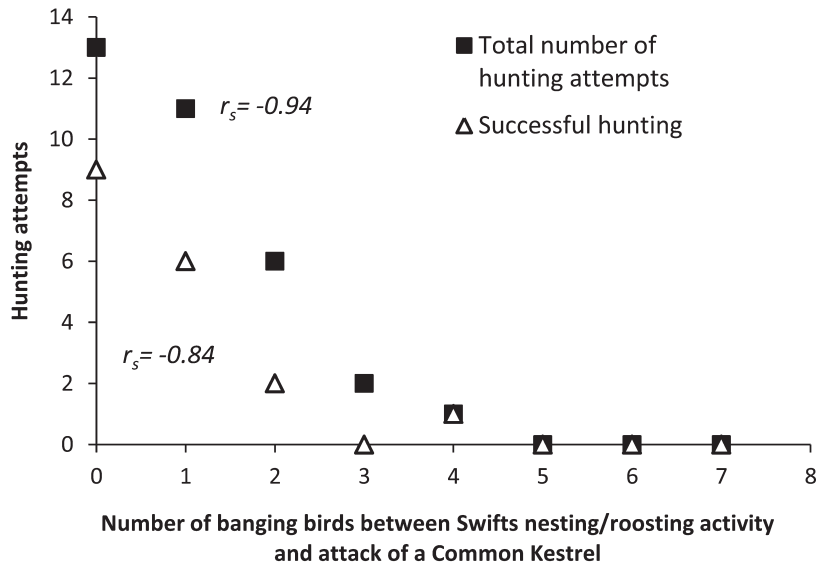


Fig. 3. Correlation between the hunting success of Common Kestrels and the number of Common Swifts showing banging behavior.

sohn 2005). Below, I discuss the evidence for, and likelihood of, each proposed explanation and propose a novel function, antipredator behaviour.

4.1. Explanation 1: Yearlings visiting their natal nests

This is one of the oldest interpretations of banging behaviour (Cutcliffe 1955, Lack 1956, Farina 1980). Yearlings arrive to the colonies in mid-June (Kaiser 1992, Tigges 2000, 2002, 2006) whereas banging behavior was observed since the beginning of May when there are only mature birds inside the colony area (Lack 1958, Tigges 2001, 2006). Thus, the explanation of yearlings visiting their natal nests is unlikely. Furthermore, up to 11 birds have been observed to show banging behaviour one after another: Thus it is rather unlikely that all of them were raised in the particular nest site the previous year, even in case of secondary brood (Lack & Lack 1952, Thomson *et al.* 1996, Kaiser 2004). Also, the breeders were found to spend their nights in the nests, whilst the non-breeders (including yearlings) mostly spent the night on a wing (Tarburton & Kaiser 2001), suggesting that banging behaviour at dusk (when banging behaviour was observed most frequently) was more likely to be shown by the breeding individuals. Finally, banging behaviour was often directed towards conspecifics, rather than the nest

sites, and towards locations which surely were not nesting sites. All these observations suggest that the explanation based on yearlings' activity is rather insufficient.

4.2. Explanation 2: Checking for unoccupied nesting sites by birds of a different age

Banging behaviour was observed from May to August. In central Europe, during the end of May most of the nesting sites are occupied (Lack & Lack 1952, Lack 1956, Tigges 2006, 2007). In a year with poor weather conditions, timing of nest site occupation (and thus inspecting nest sites) may extend up to 20 days (Tigges 2006, Thomson *et al.* 1996), but it is still unlikely that adult birds check for free nest sites in July and the beginning of August. Also, replacement broods are rare and late/extended broods are more frequent (Lack 1956, Chantler & Driessens 1999, Kaiser 2004), making it further unlikely that nest checking would continue until August. Common Swifts are also faithful to their nests (Lack 1958, Chantler & Driessens 1999), which decreases the likelihood for checking other nests (using banging behaviour)

Voice signalling has been reported as a method of nest checking (Bretagnolle 1993, Tigges 1995), but banging (with signalling) toward sites not suitable for nesting, like roof corners and balcony bal-

ustrades or walls without potential gaps for nesting, suggest that banging behaviour is unlikely to be used as nest checking.

4.3. Explanation 3: Immature birds imitating adult breeders

If banging was presented by the breeders and non-breeders alike, then the relationship inside a typical colony between these two groups should be studied further, because the data currently available is contradictory concerning at what age the swifts start to breed (Lack 1956, Perrins 1971, Kaiser 1992) and how many of the one or two-year old nonbreeders return to their natal colony the following year (Lack 1956, Tarburton & Kaiser 2001). None of the birds were seen to break away from the screaming party flights to perform banging behavior, yet some banging behavior was displayed during the same time as the screaming parties activity (some birds participating in screaming parties did perform banging behaviour just after). As nonbreeders are forming the screaming parties (Farina 1980, Tigges & Mendelssohn 2005, Blincow 2010), engaging up to half of the flying birds in the colony (own observations), which of the birds were banging at that time? Furthermore, banging behaviour was observed in the beginning of May, when breeding birds are the only birds so far in the colony. Finally, banging behavior was observed during dusk, when nonbreeders would have gone for aerial roosting, thus banging behaviour during this period can only be expressed by breeding birds (Bruderer & Weitnauer 1972, Tarburton & Kaiser 2001). Therefore, immature birds imitating the breeders also cannot be considered as a complete explanation.

4.4. Explanation 4: Intraspecific aggressiveness

Common Swifts can show high territorial aggressiveness, especially at the beginning of the breeding season (Lack & Lack 1952). Intraspecific nest box fights frequently occur (Roper 1960, Kaiser 1992). Therefore, observed physical pulling during banging may be considered as an aspect of territorial aggressiveness (Farina 1980). It has

been suggested that non-breeding birds act aggressively to reserve the future nest holes (Lack 1956, Farina 1980, 1988; Tigges & Mendelssohn 2005). However, during this study no chasing or fighting while flying was observed, even if banging behaviour ended with grabbing or pecking. Furthermore, it could be considered that up to four birds could act aggressively at one nest hole, as competing pairs. However, more than four birds were observed showing banging behaviour simultaneously, which is unlikely to present purely territorial aggression. Finally, aggressive behavior is unlikely in cases where banging behaviour was directed towards locations that could not serve as nesting sites, which often happened.

4.5. Explanation 5: Colony controlling

Due to their anatomy, swifts cannot sit and observe, and are unable to walk (Chantler & Driessens 1999). Thus, flying towards the objects of their interest is a way to examine them (Vleugel 1952), often accompanied with sound signalling (Lack 1956, Bretagnolle 1993). If banging behaviour would be associated with such behaviour, typical characteristics of banging behaviour, such as flying in groups and clinging towards walls or locations which conspecifics previously visited, is difficult to explain. It can be questioned if there is any information value for a bird, which was for example the fifth or sixth to be a banger just for one second, and repeating such behaviour throughout whole season at the same locations.

4.6. Explanation 6: “A flock of two”

Tigges (2000) observed a breeding pair entering the nest one just after another, flying so closely to each other that it was hard to recognize if there were one or two birds flying. Usually one of them enters the nest, while the second is accompanying. Such behavior was observed at AK Estate colony too, especially in late evenings of May and June. This behavior fulfils the criteria of banging behavior. Lima (2009) suggests the benefits of cooperative behaviors of a breeding pair creating “a flock of two”. In the case of banging behaviour such explanation might be correct, if a strong benefit

would be found. This leads to the final proposed explanation.

4.7. Explanation 7: Antipredator behavior

Nest predation is one of the most crucial factors in determining the birds' biology and behavior during nesting (Lima 2009). Due to the outstanding flight ability of Common Swifts, they are difficult prey for most of the hunting birds, as long as they are in the air (Hedenström & Rosen 2000, Henningsson *et al.* 2010). They lose their advantage when it comes to taking care of the nest. Although cavity nesting is one of the safest modes of breeding, it does not protect from specialized avian predators like Common Kestrels. This species has learned to hunt swifts from their cavity nests (Speelman *et al.* 1995, Mikula *et al.* 2013). Most Common Kestrel hunts were noted in the evenings, when adult birds return to the nests for the night or to feed the nestlings. Banging activity also reached its peak in the evenings. Since Common Swift nests are often hard to reach due to the narrow entrance and because these birds are clumsy on climbing the walls, it sometimes takes a few seconds for them to hide. This gives enough time for the Common Kestrels to notice them and attack (or to recognize the location of the nest). While a Common Swift individual that enters a nest becomes vulnerable and defenceless, having its head inside the hole and rest of the body outside, other birds can take the helper role (Skutch 1960) via banging behavior.

Banging behavior may result in two possible effects: A bird having difficulty getting into the nest may be pulled out by a banger and therefore get into the air, where it is much safer. This happened more frequently when it took a longer time to enter a nest, and was directed toward birds, which had not hidden completely inside the nest (with a part of wing or tail protruding), similar to the observations made by Farina (1988). Secondly, banging behaviour might serve as distraction. Several birds flying in the surroundings of a conspecifics attempting a nest entry, may camouflage its presence. Collected data seems to affirm such assumption: The more birds showed banging behavior, the less attack attempts were observed. Also, the number of successful attacks decreased with increasing number of individuals showing bang-

ing behavior. This might explain why Common Swifts exhibit banging toward places which are not their nesting sites. Banging, as a regularly repeated flying pattern, by several birds involving random locations can dishearten the predators from inspecting of such locations. Better understanding of the banging could be achieved from the wintering grounds of this species and from colonies where there are no predators like Common Kestrels.

4.8. Conclusions

All observations and hypothesis explain this particular behavior to some extent, however, they do not cover the subject completely. The antipredator benefit against Common Swift's most frequent bird of prey, the Common Kestrel, seems to play a key role in understanding generality and intensity of this behavior. Banging may discourage (confuse) predators to hunt but also reduce the success rate as the number of successful attacks decreased with increasing numbers of Common Swifts showing banging behaviour just before the Common Kestrel's attack.

Selittääkö petojen välttäminen tervapääskyn (*Apus apus*) lajiyypillistä lentokäyttäytymistä?

Jotta eläimet voivat välttää saaliiksi joutumisen, on kehitynyt laaja kirjo erilaisia petojenvälttämiskäyttäytymismalleja. Tervapääskylle (*Apus apus*) tyypillinen käyttäytymismuoto on lento, jossa yksilöt melkein pysähtyvät kesken lennon, nk. ”banging” (engl.). Tällaista käyttäytymistä havaitaan esimerkiksi saman lajin yksilöitä kohtaan, kun ne ovat siirtymässä pesä- tai lepopaikkaan, tai kun ne pysähtyvät esimerkiksi rakennuksen seinälle. Usein useampi saman lajin yksilö toistaa samaa lentokäyttäytymistä. Tälle käyttäytymismallille on esitetty useita vaihtoehtoisia selityksiä, jotka ovat melko epäjohdonmukaisia.

Tässä tutkimuksessa selvitetään vaihtoehtoisia selitysmalleja tälle käyttäytymismallille, sekä esitetään uusi selitysmalli – mahdollinen petojenvälttämiskäyttäytyminen tuulihaukan (*Falco tinnunculus*) saalistuksen välttämiseksi. Tervapääskyjä havainnointiin touko-syyskuussa 2014 ja tuoko-

elokuussa 2015 Puolan Opolessa. Yhteensä kirjattiin 1 367 havaintoa linnuista siirtymässä pesimä/lepopaikkaan, näistä 868:ssa havaittiin edellään mainittua käyttäytymistä ja 37 tuulihaukan saalistusyritystä. Mitä useamman yksilön havaittiin toistavan ”banging”-käyttäytymismallia, sitä pienempi oli tuulihaukan saalistusyritysten määrä. Tutkimuksessa selvitetään ympäristötekijöitä, jotka selittävät käyttäytymismallin ilmenemistä, ja arvoidaan eri selitysmallien todennäköisyyttä.

References

- Blincow, J. 2010: Primary purpose of Common Swift *Apus apus* screaming parties. — *Apuslife* 4950: 1.
- Bretagnolle, V. 1993. Call types of the Common Swift *Apus apus*: adult call given at the nest. — *Avocetta* 17: 141–146.
- Bruderer, B. & Weitnauer, E. 1972: Radarbeobachtungen über Zug und Nachtflüge des Mauerseglers *Apus apus*. — *Revue Suisse de Zoologie* 79: 1190–1200. (In German)
- Chantler, P. & Driessens, G. 1999: Swifts: A guide to the Swifts and Treeswifts of the world. — Pica Press, Sussex.
- Cutcliffe, A.S. 1951: Notes of the breeding habits of the Swift. — *British Birds* 44: 47–56.
- Cutcliffe, A.S. 1955: Further notes on the Swift, 1944–1955. — *British Birds* 48: 193–203.
- Farina, A. 1980: Some observations on the social behaviour of the Swift *Apus apus* (L.) during the breeding season. — *Monitore Zoologico Italiano* 8: 235–244.
- Farina, A. 1988: Observations on the Swift's *Apus apus* (L.) social flights at the breeding site. — *Monitore Zoologico Italiano* 22: 255–261.
- Hedenström, A. & Rosen, M. 2000: Predators versus prey: on aerial hunting and escape strategies in birds. — *Behavioural Ecology* 2: 150–156.
- Henningsson, P., Johansson, L.C. & Hedenström, A. 2010: How swift are swifts *Apus apus*? — *Journal of Avian Biology* 41: 94–98.
- Kaiser, E. 1992: Populationsdynamik einer Mauersegler *Apus apus* Kolonie unter besonderer Berücksichtigung der Nichtbrüter. — *Die Vogelwelt* 113: 71–81. (In German)
- Kaiser, E. 1997: Sexual recognition of Common Swifts. — *British Birds* 90: 167–174.
- Kaiser, E. 2004: Gehäuftes Auftreten von Zweitbruten beim Mauersegler. — *Die Vogelwelt*. 125: 113–115. (In German)
- Lack, D. & Lack, E. 1952: The Breeding Behaviour of the Swift. — *British Birds* 45: 193–195.
- Lack, D. 1956: Swifts in a Tower. — Mathuen and Co., London.
- Lack, D. 1958: The return and departure of Swifts at Oxford. — *Ibis* 100: 477–502.
- Lima, S.L. 2009: Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. — *Biological reviews* 84: 485–513.
- Mikula, P., Hromada, M. & Tryjanowski, P. 2013: Bats and Swifts as a food of the European Kestrel (*Falco tinnunculus*) in a small town in Slovakia. — *Ornis Fennica* 90: 178–185.
- Perrins, C. 1971: Age of first breeding and adult survival rate in the Swift. — *Bird Study* 18: 61–70.
- Roper, E.N. 1960: Swifts fighting. — *British Birds* 53: 447.
- Rothgänger, G. & Rothgänger, H. 1973: Über spezielle Verhaltensweisen fliegender Mauersegler. — *Der Falke* 20: 124–130. (In German)
- Speelman, R., Jong, L. & Hasper, H. 1995: Adult Swifts *Apus apus* as prey of Kestrel *Falco tinnunculus*. — *Drentse Vogels* 8: 18–20.
- Skutch, A.F. 1960: Helpers among birds. — *The Condor* 63: 198–226.
- Tarburton, M.K. & Kaiser, E. 2001: Do fledgling and pre-breeding Common Swifts *Apus apus* take part in aerial roosting? An answer from a radio tracking experiment. — *Ibis* 143: 255–263.
- Thomson, D.L., Douglas-Home, H., Furness, R.W. & Monaghan, P. 1996: Breeding success and survival in the Common Swift *Apus apus*: a long term study on the effects of weather. — *Journal of Zoology* 239: 29–38.
- Tigges, U. 1995: Kann man Mauersegler gezielt ansiedeln? — *Der Falke* 42: 250–252. (In German)
- Tigges, U. 1999: Das täglich letzte Einfliegen der Mauersegler (*Apus apus*) in Abhängigkeit von Brutphänologie, Umwelt- und sozialen Faktoren. — *Berliner ornithologischer Bericht* 9: 49–58. (In German)
- Tigges, U. 2000: Mauersegler in Berlin und Brandenburg. — *Apuslife* 2405.
- Tigges, U. 2001: Departure and arrival of Common Swift *Apus apus* in Tel Aviv, Israel, in 1999–2000. — *Sandgrouse* 23: 59.
- Tigges, U. 2002: The Migration of the Common Swift *Apus apus* to its breeding areas. — *Osprey* 2: 19.
- Tigges, U. 2006: The breeding cycle in calendar form of the Common Swift *Apus apus* across its Eurasian breeding range – a testable hypothesis? — *Podoces* 1: 27–33.
- Tigges, U. 2007: The phenology of the Common Swift *Apus apus* in Eurasia and the problem of defining the duration of their stay. — *Podoces* 2: 127–140.
- Tigges, U., Mendelssohn H. 2005: Phenology and Behaviour of the Common Swift *Apus apus* in Israel. Holy Birds, or the Common Swifts of Jerusalem's Western Wall. — *Sandgrouse* 27: 82–87.
- Vleugel, D.A. 1952: Nestplatzzeigen und Scheinkopulation beim Mauersegler im Juni und Juli unter Berücksichtigung des Alpenseglers. — *Die Vogelwelt* 73: 13–16. (In German)