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Epimeletic behaviour in airborne Common Swifts *Apus apus*: do adults support young in flight?

Epimeletiskt beteende hos flygande tornseglare Apus apus*: hjälper vuxna de unga i flykten?*

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Abstract

Seven cases of presumed epimeletic behaviour of adult Common Swifts toward flying young were recorded. The behaviour varied from adults escorting the young, over episodes when part of the colony swirled around the newcomer, to instances when an adult touched the young from below. A flying dummy was also encircled when exposed to adults. An eighth case was a non-aggressive behaviour of a migrating Swift toward a fledged soliciting House Martin. The behaviour seems to be a parallel to the care-giving (epimeletic) behaviour in cetaceans, e.g. dolphins, and is therefore seen as an airborne epimeletic behaviour. The Common Swift and dolphins have adapted to elements which are extreme to birds and mammals. If a Swift fledgling falls to the ground or a newborn dolphin (or an injured adult) sinks in the water, each will succumb. Over evolutionary time, therefore, epimeletic behaviour should have been favoured. The identical behaviour of adults of different animal taxa in different environments is here seen as behavioural convergence.

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Introduction

When young Common Swifts *Apus apus* make their first, unsteady flight, they may be approached rapidly and closely by adults of the colony. This behaviour has been interpreted as aggressive (e.g. Goethe 1939). Here we report on such behaviour but interpret it as epimeletic.

Epimeletic (Greek: care-giving) behaviour (Scott 1958) has been studied extensively in cetaceans (whales, dolphins and porpoises) (Caldwell & Caldwell 1966, Connor & Norris 1982, Gowans, Würsig & Karczmarski 2007). Care-giving is widespread in vertebrates including fish and in invertebrates e.g. insects (Guyot 2004). In this sense, it means feeding, protecting and/or defending offspring by parents. In a more specific sense, as studied in cetaceans, epimeletic behaviour is care given by adults, often collectively, to adults and non-relatives as well as to offspring, as a response to care-soliciting behaviour (Scott 1958, Caldwell & Caldwell 1966).

Following Scott (1958), Caldwell & Caldwell (1966) discriminated between two types of epimeletic behaviour in cetaceans, "nurturant" if care is directed toward young, and "succorant" if directed by adults to adults. Succorant behaviour was broken down into (i) "standing by" which is to remain in or approach the area of a distressed species member but without rendering assistance, (ii) "excitement" includes approaching an injured comrade and showing hyper-excitability or distress , and (iii) "supporting behaviour" is when one or more animals support an injured individual in body contact at the surface. Distress may be vocalized or silent (Caldwell & Caldwell 1966). Succorant behaviour involving two different species has sometimes been seen (Caldwell & Caldwell 1966) which has been characterized as "spill-over" reactions (Norris & Dohl 1980).

Like many cetaceans, Swifts are gregarious and live in large colonies where nesting sites abound. Similarly, they join in coordinated social behaviour, e.g. what is known as "screaming parties" which circle the breeding place. Swifts are adapted for high speed flight and an airborne life. Compared with most other aerial feeders as hirundines (e.g. House Martin *Delichon urbica* and Barn Swallow

Hirundo rustica), Swifts have a low manoeuvrability and are unable to fly at lower speeds (Chantler 2000, Henningsson, Spedding & Hedenström 2008). Swifts spend most of their time in the air, occasionally also mating there as well as roosting at high aerial altitudes (Bromhall 1980, Tarburton & Kaiser 2001, Bäckman & Alerstam 2001; see also Holmgren 2004). If fallen to the ground, a Swift with its long wings and short legs will get on the wing again with some difficulty (young Swifts, see Schulte 2000). Swifts exist under conditions which are imperative and similar to those of cetaceans in spite of the two animal classes living in two different elements, however both fluid and non-supporting, i.e. if not at once being able to fly or to swim, respectively, the young will fall victim to predation (Figure 2) or drown.

Our observations are from central Sweden. Most of them were made in companionship with named witnesses (see abbreviations and Acknowledgements). By comparing with cetaceans, we put Swift behaviour in an evolutionary context. In spite of technical difficulties with respect to documentation (see below), we see the possible prevalence of epimeletic behaviour in the Swift as a hypothesis that should be testable.

Observation sites and observation opportunities

The observations span more than 30 years. Most of them were made at a summer house named "Rian" at Frösåker, Västerås Commune at Lake Mälaren (59º 32' N, 16º 44' E) and some at Mosstorp, a homestead at Almunge, Uppsala Commune (59º 55' N, 18º 08' E). Rian is situated on an "islet", about 150×60 m in size, formerly surrounded by arable land, since 1989 by a golf course. The "islet" is directed in an approximately N–S direction (Figure 1). Eight hundred metres to the SE lies the Frösåker cove which is a part of Lake Mälaren. The "islet" is surrounded to the N, W and SW by groves and beyond those there are forests. To the NE and E there is open land as also to the SE right on to the cove.

The roofs of the buildings on the "islet" are of convex tiles. Varying over the years, three to five pairs of Swifts have nested under the tiles of Rian or in openings under the eave (4 m above ground). In recent years, single pairs have also bred under the tiles of the smithy and the privy (Figure 1; 2–2.5 m above ground). One pair regularly breeds in hollows high up in each of the two oak trees (Figure 1). Furthermore, one or two pairs have every year bred under the tiles or the eave (Figure 1; about 3.5 m above ground) of the cottage (most breeding evidenced from droppings). Thus, screaming parties of about 20 birds may circle the Rian and sometimes more than 50 birds may join over the site. Every year, House Martins colonize the mill and from time to time also the transformer house and the barn. Occasionally, however not in recent years, Barn Swallows have bred in the smithy.

Mosstorp is a small farm homestead situated on the southern slope of a moraine ridge extending in a roughly N–S direction. About 50 m north to the house there is a coniferous forest, whereas the rest of the vicinity is open fields. Like at Rian, the roof is tiles, but, in addition, about 10 nest-boxes have been erected on the walls (approx. 4 m above ground) to facilitate for the Swifts to breed. Despite the tiles being freely accessible to the Swifts, no single pair has ever bred under them. Instead eight pairs breed in the nest boxes. Just as at Rian, the Swift population in the surroundings is reasonably large, and screaming parties of 30–40 birds are frequently seen around the Mosstorp homestead.

The "next door" neighbourhood to the Swifts has offered opportunities for chance observations. Once suspicion of epimeletic behaviour in the Swift arose, summer residents on the Rian "islet" have become more observant on peculiarities in Swift behaviour and have joined in an intermittent and informal observation team. This also implied that when fledglings were found on the ground, they were handed over to one of us (O.T.) for hand-raising. They were fed balls of vitaminized and moistened mince (however, for a more suitable food, see Matthes 2006) mixed with small insects when such were available or with commercially available ant pupae. Three of the few juveniles picked up (7 juveniles over >30 years, including one which could fly immediately), died soon because they were too exhausted or severely injured. The three birds which grew to be fledged were released, if possible when members of the Swift colony were flying in the vicinity to see the reactions of adults towards the young bird. When released, the birds were gently passed into the air. No release was made at Mosstorp.

Some experiments were performed in the 1980s and 1990s. In order to elicit responses of flying adults, a free flying dummy with rubber-band driven flapping wings was used (a toy named "Tim de Ruymbeke" by Ets G. de Ruymbeke, Marseille, France). Two models were tested, the original toy and a toy specimen reshaped to and coloured as a fledgling and of the same wing span, i.e. 40

Figure 1. A bird's-eye view of the "islet" where the behaviour of Common Swifts was observed. Buildings named in the text are the "transformer house" at the southern end of the "islet", the "smithy" and the "privy" just north of Rian, and the "cottage" at the northern end. At each of the cottage and the Rian an old oak tree is growing. The elongated building with a pointed roof is the "mill" and the large building to the east, the "barn". At the southern margin of the photo three ponds are seen. The "grove" is at the western margin just south of the narrow, E-W running road. (Copyright: Lantmäteriet, SE-801 82 Gävle, Sweden.)
Observationsområdet Rian ur fågelperspektiv.

cm (Figure 2). Apart from giving opportunities to observe responses of adults present, the intention with the model experiment was to take photos of responses. These experiments were performed at Rian and Mosstorp. Reactions were seen but photographing failed due to the short duration of the flight of the models. In 2007, various free flying fixed-wing aeroplane models, propeller-driven by in-built electrical batteries, were also tested at Rian. Their wing-spans were from 30 to 45 cm. The models (Silverlit Electronics) were commercially available.

In addition, a request for independent observations was sent out on a national level by the web sites of Club300 Brevduvan and SOF (The Swedish Ornithological Society) on 30 January 2008. Two observations were received, one reported below under Independent observation and one under Discussion.

Figure 2. The dummy and the original toy model used to elicit epimeletic behaviour in Swift. On top, remains of a Swift fledgling that fell victim to a raptor close to the "Rian" (July 2007).
Modellen och leksaken som användes i försöken att utlösa epimeletiskt beteende hos tornseglarna. Överst resterna av en flygg unge som föll offer för en rovfågel vid Rian i juli 2007.

Observations with fledglings

There are seven observations of notable behaviour of Swifts towards fledglings and one towards a Swift of unknown age.

(1) *Undated observation, probably in 1974 or 1975*. An almost full-grown fledgling was found on the ground near the barn. It was hand-raised (M. M. and R. M.) and subsequently released from the "islet". It was conspicuous, and therefore noted, that when it ascended above the cottage and the oak tree at the northern end of the "islet", it was accompanied tightly from below as well as vividly encircled by adult Swifts. (M.M)

(2) *17 July 1979*. The following observation gave rise to the idea of epimeletic behaviour in the Swift. A well developed fledgling was found on the ground beneath one of the nests on the southern side of Rian. In this case the young bird was thrown straight off into the air toward a stubble-field between Rian and the barn. The bird lost height rapidly and the flight seemed to end on the field. Simultaneously, an adult Swift began a fly-in to the nest and met the fledgling. The adult immediately turned and caught up with the fledgling and touched it two or three times. This occurred very rapidly. For each touch, the young bird gained height and finally reached a secure altitude. Tightly encircled by several adults, it wheeled above the field between the "islet" and the barn until it and the flock, which thinned successively, disappeared towards the Frösåker cove. The young bird was distinguished from its somewhat smaller size and blunt wing tips. This occurred at day-time, the sky was overcast and there was a weak wind from south (O.T. and C.T.)

(3) *Undated observation from the early 1980s.* In 1980–1997 surveillance was less effective. Two of the three young Swifts which died (see above) were picked up during this period. However, there is one incidence:

One Swift had been trapped in the loft of the cottage, the bird probably coming from one of the two usually inhabited nests under the roof. The loft was dark except for the day-light from a window at the southern gable. Outside the gable several Swifts were circling. When the window was opened, the trapped Swift flew out and was immediately encircled by Swifts "as if they waited for the bird". The observer supposed that the Swifts outside could have seen the trapped bird through the window. Whether the Swift was an adult or a fledgling is not known (E.L.).

(4) *15 August 1998.* On 19 July, a young Swift, still with blood quills was found on the ground at the western side of the Rian. The young was raised until it seemed fully grown and made spontaneous attempts to fly. Our intention was to release it in the presence of adults. However, we had to leave in the middle of the day when all adults were away. After having been hand-launched on the western side of the Rian, the young bird first lost height heading towards a pond on the golf course. Just before crashing into the water, as it seemed, it turned north and ascended and reached the "grove" (Figure 1) at about tree height where it turned south. At that moment, an adult precipitated from the upper air-space, flew along-side and tightly with the young for a while and then returned to upper air. After this short visit of the adult Swift, the young Swift wheeled once more over the golf course then headed towards the cove at increasing altitude. After having passed the mill, it was again visited shortly by an adult coming from above. Then the young bird was out of sight. No voices were heard from the Swifts. It was impressive to see how rapidly the fledgling improved its flight, from being unstable initially and with rapid wing-beating, to be balanced and effective, even with intermittent gliding. (O.T., C.T., B.T., B.H. and A.H.)

(5) 13 August 2000. A nearly full-grown fledgling was found on the ground on the northern side of the Rian on 8 August and was hand-raised. In the afternoon of 13 August, it was thrown into the air over the golf rough W of Rian. It took well on the wing, turned around the transformer house and passed the mill. We followed it running. When the fledged young approached the barn and flew over it, adults met, probably coming from a flock shortly before seen SE of the barn. The young bird gained height, seemingly from touches (D.M.). It may have heard this flock already when released and therefore headed towards it. (O.T., R.M., J.M. and D.M.)

(6) *29 July 2002.* In the evening there was great excitement among more than 50 Swifts that swarmed at the southern side of the Rian. At about half an hour after sunset, one of the nestlings that previously had been peeping out from its nest-hole under the roof on the southern side, flung itself into the air and flew towards the transformer house. Against the bright sky, we could see that an adult Swift touched the young bird so that it staggered a little. From the beginning, several adults escorted it until finally only one stayed at its side when the birds came out of sight. The young bird had a smaller wing-span than the adult Swifts, looked fatter and flew unsteadily. The sky was clear, it was

warm (18–19ºC) with a weak wind from E. (O.T. and D.M.)

(7) *2 September 2007*. At about 2:15 p.m., a Swift was seen making fly-ins towards the eastern gable of Rian. When checking, we discovered that a new-fledged House Martin perched in the small space between the roof ridge and the top of the vertical mid-stock of the eastern gable. The sky was overcast and the weather windy with intermittent light rain from SW. The fledged bird had probably come from the colony of House Martins breeding under the roof of the mill and had made an emergency landing for shelter. Several adult Martins still occurred at the mill. During about a quarter of an hour, the Swift made more than five fly-ins towards the fledgling, coming from the open area to the east. It did not take hold but just passed and turned out again about half a meter from the young. Now and then an adult House Martin flew in and fed the young bird which was constantly calling and sometimes begged with shivering wings. Photos were taken of the House Martin and the Swift but we did not manage to document the meeting of the two birds and did not catch whether the intense begging was also directed towards the in-coming Swift. Finally, the Swift left. (O.T. and B. T.)

(8) *Independent observation* (Stefan Asker, answer 31 January 2008 to a national request). "This occurred two or three years ago at our summer house at Seberneby on the "Alvar", an open area in the southern part of the Isle of Öland. My daughter found a Swift on the ground beneath the tiles under which the birds breed. It was a young bird, typically with unworn light-bordered feathers. I launched it into the air. Immediately, one of the adult swifts came to assistance and very clearly pushed the young repeatedly from below. Another Swift flew rather close to the young. After the pushing, the young circled around with the 10 or so adults of the colony. At the beginning, the flight of the young was unsteady but together with the adult Swifts it rapidly became easy. It was in July/August on a sunny morning with clear sky. The tiles under which the Swifts breed are 2.5–3 m above the ground. There are low apple trees and bushes around the house and there are no other houses in the vicinity except for an old stone building."

Experiments with dummies

Swifts reacted to both variants of the rubber-band driven model. The dummy was thrown into the air or launched from the roof of Rian and the house at Mosstorp. When the flapping dummy sank toward the ground, Swifts dived collectively towards it, in cases even down close to the ground before they ascended (Mosstorp, 2 June 1982). The tests gave similar results in both colonies. Reactions occurred in early June as well as in July and early August. It was further noted that passing Barn Swallows (in summer) and migrating Swifts in August did not respond. However, the frequency or intensity of these reactions or the lack of reactions was not studied systematically. Preliminary observations with the fixed-wing models indicated that they were less enticing than the flapping models.

Discussion

At our sites, Swifts nest a few metres above ground close to people in an open landscape (Figure 1) where the course of events can be followed even on foot (15 August 1998; 13 August 2000; 29 July 2002). Thus, we have ample opportunities to observe Swift behaviour at close distance, which is not always the case in urban areas. In addition, in most cases, fledglings were released when adult Swifts were present (undated observation 1974/1975; 17 July 1979; 29 July 2002). This also applied to the independent observation and the dummies. We have seen Swifts coming in from far away (15 August 1998) as well as from ambient air space (29 July 2002) to fly alongside fledglings on their first flight. In another observation, the fledged young and adults may have sought each other from a distance (13 August 2000). The short meetings of a fledged young and adults on the 15 August 1998 were the most clear cut case of a seemingly epimeletic behaviour because it was not followed by any other behaviour of the adults. Observations of similar kinds were reported by Tarburton & Kaiser (2001). They wrote: "The three (young) that we induced to fly all left within 20 min. One went up and was met momentarily by two others and then headed west. The second was also closely inspected by another swift for a moment [.....]. The third one was the orphan and it too was given a welcoming inspection by another swift as it flew to the west". In three cases (the two undated observations and 17 July 1979) and in the independent observation, part or all of the Swift colony engaged in vivid circling around the newcomer as well as in one of the dummy experiments when adults followed the dummy close to the ground.

Some of the circlings were preceded by body contacts (17 July 1979, 13 August 2000, 29 July 2002). These touches were very rapid and it was not possible to catch from which direction they

came. In the case of the 17 July 1979 observation, the fledgling should at once have tumbled down to the ground if the touches had been from above and aggressive as we thought instantly. Instead, it gained height. Thus, we concluded that the touches were from below. The same applies to the observation on 13 August 2000. These indications are substantiated by the distinct pushing from below seen by Stefan Asker (Independent observation). One purpose of provoking adults to react on the dummies was to take photos of touches (which failed, see above) and by that document from which direction they came.

The reaction of the Swift to the fledged House Martin on 2 September 2007 is hard to interpret. The "islet's" own Swifts had left already in the middle of August and the Swift should have been a migrating individual which continued its migration after the visit. It was a day of gusty winds and intermittent light raining. Normally, fly-ins for roosting occur well after sunset in late summer (Holmgren 2004). In this case they occurred in daylight in early afternoon. The vigorous flight of the Swift and the many fly-ins without any attempt to hang up indicated that it neither intended to roost for the day nor to perch due to exhaustion. The Swift is an aggressive bird and it could easily have chucked out the House Martin as we have seen Swifts do with chicks and nests of the Spotted Flycatcher *Musicapa striata* nesting on the top of the vertical mid-stock of the western gable of Rian. However, fights among Swifts or with House Sparrows Passer domesticus or Tree Sparrows *Passer montanus* mainly concern nesting places after the Swifts´ arrival to breeding grounds in early summer. Thus, it seems unlikely that a migrating Swift in September should spend time and energy on any aggressive behaviour.

Swifts sometimes harass birds of prey that pass their air territory, i.e. following or circling around the predator, although from a respectful distance. Could the reactions to the dummies have been harassment? The shape of the dummies was the same as that of a Hobby *Falco subbuteo* however with a wing-span of only half of the Hobby´s (Figure 2). We have seen Hobbies both take and un-successfully chase Swifts at Rian (O.T.) and at Mosstorp (T.F.) (cf. Figure 2). Because the Swifts approached the dummy very closely rather than keeping a distance, we assume that the responses of adult Swifts to the flapping dummies were of the same kind as their responses to fledged young (if not of curiosity or just for fun). On the other hand, when confronted with the fixed-wing models which fly rapidly and excellently, the Swifts may have hesitated to approach.

Obviously, as we see it, there is a remarkable parallelism in the behaviour of the Swift with caregiving in cetaceans. Therefore, the terminology for cetacean behaviour is applied to the Swift. Accordingly, the "well-coming" (Tarburton & Kaiser 2001) and escorting of the young that we have seen (15 August 1998 and 29 July 2002), as well as the reactions to the dummies, are assigned to "standing by" and the vivid circling of colony members around newcomers (the two undated observations, 17 July 1979 and 13 August 2000) and the dummy to "excitement". The pushing from below of new-fledged birds by adults is seen as "supporting behaviour" (17 July 1979, 13 August 2000 and the independent observation). Concerning the repeated fly-ins of the Swift towards the new-fledged House Martin on 2 September 2007, we note that this occurred across the border between two widely separated taxa (Apodiformes and Passeriformes) but make no interpretation other than that the behaviour seems to have been non-aggressive.

We have found four published observations on similar behaviour as we have described here. One is the "welcome" ceremony reported by Tarburton & Kaiser (2001, see above). Two others are on adults touching fledglings wing to wing or flying close to them (Wendt 1988, Hampe 1990). This occurred regularly when the young were hand-launched at day-time, in several cases far from where the young were born (Hampe 1990). According to both observers, it is unlikely that the touching or escorting adults were parents to the fledglings. This should also apply to the adults observed in 1974 or 1975 (undated) and on 15 August 1998. Compare also the reactions of the Swifts to the dummies. The fourth is by Goethe (1939), see below. Thus, attention may be collective just as in dolphins (e.g. Gowans et al. 2008). Perrins (2002) notes that fledglings may not receive further parental care from the moment that they leave the nest. However, we hypothesize here that a form of care resembling epimeletic behaviour in cetaceans may indeed prevail in Swifts, although the evolutionary explanation may be different.

All observations except one (29 July 2002) were made at day-time when adults are on the wing to meet fledglings. However, the large majority of fledglings depart at late dusk when no parents or adults are around (Kaiser 1984, Perrins 2002, Erich Kaiser pers. comm.). This may seem incompatible with any evolution of an airborne care. Nonetheless, the observed behaviour is repeated in a stereotyped manner, whether a fledgling is hand-launched at

day-time or departs spontaneously at dusk, or when a dummy is launched. This indicates a long adaptive tuning.

It is notoriously difficult to study Swifts and cetaceans in their natural elements, the upper air and the deep sea water. Much of their behaviour therefore remains unknown. The reasons for the scarcity of published reports on adult/fledgling interactions in the Swift are at least five-fold: Swifts have nested under tiles close to Man for only a short time (in Sweden, mainly since the beginning of the 19th century after tiles were introduced: Fagerström 1988, Svensson 1999), optimal local setting for observations is rare, the different types of behaviour are rare, they occur very rapidly, and naturalists observing them are rare. In contrast, written-down hearsays on cetacean behaviour go back into antiquity (Aristotle, in Caldwell & Caldwell 1966), followed by evidences told by whalemen and in recent time replaced by scientific documentation (e.g. Kellogg 1961, Caldwell & Caldwell 1966, Norris & Dohl 1980, Connor & Norris 1982). Such meetings with the large and, compared with Swifts, slow-moving animals have offered opportunities to observe behaviour details despite difficulties (e.g. Felix 1994, Ritter 2007).

A life in the air seems to have brought about a more sophisticated epimeletic behaviour in the Swift than in, e.g., passerine birds. Many passerines nest in forests and when a fledgling leaves the nest and falls to the ground, it can partly fly, partly climb a tree and reach security and there obtain continued feeding from its parents (cf. the House Martin, 2 September 2007). In contrast, the newfledged Swift has to enter the air successfully, either by itself or, according to our hypothesis, with assistance from parents and/or part of the Swift community, and thereafter feed itself.

This behaviour seems to be specific to the Common Swift (but could conceivably prevail also in other *Apus* species). To our knowledge, there is nothing the like in, e.g., passerines which obviously do not need it. As one exception, in another aerial feeder, the House Martin, both a parental and a collective airborne care of its young has evolved (Lind 1960). In a taxonomically more distant family, Alcidae (Alciformes), the fledglings of some species are in a predicament similar to that of young Swifts. When the half-grown young of the Common Murre *Uria aalge* and the Thick-billed Murre *U. lomvia* jump from high cliffs and try to fly to the sea, some drop to the stony shore between the cliff and the sea and run the risk of being severely injured or fall victim to predation. In these species and in the Little Auk *Alle alle*, parents escort their offspring during the flight to the water (Harding, van Pelt, Lifjeld & Mehlum 2004, "Ut i naturen", Norsk Rikskringkasting January 8, 2008 http://www.1.nrk.no/nett-tv/klipp/324045). In addition, there are unambiguous observations of *Uria* spp. parents pushing their fledging young from below (Lars von Konow, pers. comm., see Appendix) or carrying them airborne to the sea (Ossian Olofsson 1925, see Appendix) which corroborate old observations (Sørensen 1859, Hans Christopher Müller 1862 in von Droste 1869). It has also been shown that breeding Thick-billed Murres sometimes adopt unrelated eggs and chicks (Gaston, Eberl, Hipfner & Lefevre 1995) and, as a consequence, most probably guide these unrelated fledglings to the sea in due course.

One alternative to our interpretation is that the close approach of adults to fledged young Swifts is an act of aggression (Goethe 1939, Erich Kaiser, pers. comm., Jan Holmgren, pers. comm.). Mobbing and even killing of conspecifics that behave or look abnormal is well documented (Goethe 1939). According to the "aggression hypothesis", the initially unstably flying young Swifts are perceived to be abnormal and are therefore met with aggression. The same should apply to the Herring Gull *Larus argentatus* (Goethe 1937, p. 43). Each interpretation might include that curiosity is involved. It is a lot of subjectivity in either interpretation (cf. Swift/bat encounters, Näfe 1997) and neither can be settled until details of behaviour have been documented unequivocally. However, airborne epimeletic behaviour is found in other bird orders (see above). Pushes from below occur in alcids. The young Swift which left spontaneously at dusk (29 July 2002) did not hesitate to meet the excited flock outside. The same applies to the trapped bird (undated observation, early 1980s) which could have been an adult Swift. It is also evident that young Swifts may be visited and encircled after that a stable flight has been achieved (e.g. 15 August 1998, the independent observation). Further, the fly-ins towards the young House Martin did not seem aggressive (2 September 2007). We find that this and the parallelism with alcids point at an epimeletic rather than an aggressive behaviour and that the "epimeletic hypothesis" has the greatest explanatory power for a diversity of behaviour.

Over evolutionary time, cetaceans and Swifts have adapted to a full-time (or almost full-time) dwelling in an environment which was extreme to mammals and birds. During this time, an increasing ability to assist and prevent offspring from drown-

ing and falling to the ground, respectively, should have been a fundamental positive selective force. In dolphins there is a sophisticated parental cooperation among females. Newborn can swim but are often supported from below by the mother (Caldwell & Caldwell 1966, Darling & Taber 2001). When the foetus was expelled, adults swam under and to each side of the rising infant, apparently to secure that it reached the surface safely (Caldwell & Caldwell 1966, Connor & Norris 1982). One can note the close similarity in behaviour of Swifts surrounding the young from below and from the sides when it ascended in the air (undated observation 1974/1975). An identical behaviour in the two cases may be explained as a behavioural convergence as a response to an identical lethal threat to the newcomer in the sea and in the air, i.e. to sink.

It seems likely from the available evidence that adult Swifts will approach and attempt to rescue any fledgling as their own offspring that they perceive to be at risk of sinking to the ground. Swifts do not recognize their own offspring (Erich Kaiser, pers. comm.). Hence we hypothesize that this behaviour is to a high degree misdirected parental care (as in the Thick-billed Murre; Gaston et al. 1995) although in effect non-parental. In evolutionary terms this would imply that the adults perform a truly altruistic behaviour in case non-related fledglings are at stake, and a non-altruistic one when their own offspring are at stake. The probability of either category would be roughly a function of colony size N, with 1/N being the probability of non-altruistic behaviour and 1–1/N the probability of altruistic behaviour.

How can the seemingly altruistic behaviour be explained in terms of individual selection? We suggest that there has been an evolutionary advantage to this behaviour, despite the implied element of altruism. First, the epimeletic behaviour is likely to have been rather "cheap" for the adults, i.e. the costs of performing a rescue operation are likely to be small. Hence, from a cost-benefit point of view this behavioural trait could evolve even if the altruistic element was substantial. Second, during much of the evolutionary history of Swifts, the altruistic element may in fact have been small because Swifts originally nested in sparse tree holes (as they still do in northern Scandinavia), suggesting a small N-value (with N=1 the altruistic element disappears altogether).

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Sammanfattning

Ursprungligen var tornseglaren *Apus apus* L. en inte så vanlig urskogsfågel som häckade i glest spridda gamla hackspettshål. En revolution ägde rum när taktegel började användas allt mer från 1800-talets början. Med det större utbudet av lämpliga boplatser under det kupiga teglet kunde glesbygdsbon bli en utpräglad kolonibildare och populationerna ökade kraftigt. Tornseglarna tillhör nu våra mest synliga fåglar där de kretsar högt i det blå eller högljutt och halsbrytande formationsflyger runt husen och när andra fåglar slutat att höras, hörs tornseglarens ”screaming parties” sommaren ut.

Trots denna se- och hörbara närvaro har tornseglaren varit och är fortfarande en gåtfull och okänd fågel. Artens extrema anpassning till ett konstant luftburet liv, frånsett häckningstiden, gör den svårstuderad. Livet i luften har inneburit flera specialanpassningar som man trots svårigheterna nu känner till och har dokumenterat. Maximala flyghastigheten matchas bara av huvudfienden lärkfalken och några arter till. Fåglarna kan para sig i flykten. Övernattning sker ibland högt upp i natthimlen. Men de kan också hänga upp sig för vila på väggar och murar och i lövverk. Bland det gåtfulla finns t.ex. varför kolonins vuxna fåglar ibland snabbt och nära uppvaktar ungfåglar under flygdebuten. Det är temat för vår uppsats.

Om tornseglaren är svårstuderad i sitt rätta element är den desto lättare att komma inpå livet när den häckar eftersom den delar bostad med oss själva. Genom att inifrån och osynligt för fåglarna studera familjelivet har man lärt mycket om föräldrars och ungars beteenden. En kunskap som är relevant här är att flertalet ungar lämnar boet sent i skymningen, möjligen som en anpassning så att de osäkert flygande ungfåglarna inte ska dödas av dagrovfåglar. Man vet också att väl utflugen måste den unga tornseglaren söka föda själv.

En nackdel med den extrema anpassningen är att tornseglaren vid låga hastigheter har svårt att flyga och manövrera och skulle den hamna på marken kan den ha svårt att ta sig upp igen. De långa vingarna hindrar och den kan inte som en tätting ta sats med sina korta ben (latinets apus = utan fot). En

vuxen kan ändå komma på vingarna igen om den inte hindras av vegetationen men en flygg ungfågel kan lätt bli byte för rovdjur (Figur 2).

Här rapporterar vi om äldre tornseglares ”uppvaktning” av flygdebuterande ungfåglar och tolkar beteendet som *epimeletiskt*. Epimeletiskt (från grekiskan: vårdgivande) beteende visar de flesta djurarter mot sin avkomma, d.v.s. vårdar, skyddar och försvarar sina ägg och/eller ungar. Hos en del sociala däggdjur omfattar beteendet även vuxna individer i nöd. I den betydelsen har begreppet epimeletisk framför allt tillämpats på valdjurs beteende, t.ex. vid studiet av delfiner. Beteendet har indelats i tre underkategorier: *beredskap* (standing by), d.v.s. att valar och delfiner stannar kvar eller närmar sig en stressad flockmedlem utan att ge hjälp, *upphetsning* (excitement), att komma till en kamrat i nöd och visa oro, t.ex. genom att cirkla runt kamraten, och *stöd* (supporting), att en eller flera individer stöder, följer och lyfter upp en nyfödd kalv eller skadad medlem till vattenytan. Det epimeletiska beteendet kan också korsa artgränser och har då kallats *överspillsreaktioner* (spill-over reactions). Här jämför vi tornseglarens beteenden med främst delfiners. Jämförelsen kan tyckas egendomlig men tornseglare under sin första flygtur och nyfödda eller skadade delfiner har ett gemensamt: båda lever i flytande, icke-bärande element, luft resp. vatten, och sjunker de, riskerar de att dö. Jämförelse görs också med alkfåglar (sillgrisslor).

Observationerna gjordes vid två boställen, ett i den centrala (Figur 1) och ett i den östra delen av den mellansvenska landsbygden, vardera med cirka 10 bon i tornseglarkolonin. Möjligheterna till iakttagelser har gynnats av att husen är låga med bona högst 4 m över marken och att husen är belägna i öppna landskap. Sju observationer av anmärkningsvärda beteenden av äldre fåglar riktade mot ungfåglar noterades över ett 30-tal år. Via ett upprop inom landet fick vi också en oberoende observation (från Öland) och en om alkors beteende (Lofoten). De flesta iakttagelserna gjordes när unga tornseglare hittats på marken och kastats upp i luften, antingen efter handuppfödning eller direkt om de verkade flygfärdiga. Detta gäller också den öländska observationen. För att iaktta tornseglarkoloniernas reaktioner gjorde vi också experiment med en friflygande modell av en tornseglare (Figur 2).

Beteendena har varierat från att enstaka vuxna tornseglare kommit ner från hög höjd för att ett kort tag flyga nära och jämsides med ungfågeln innan de återvänt till det övre lufthavet (en observation), över att hela eller delar av kolonin snabbt cirklat runt och tätt under den unga fågeln (tre observationer), till att en vuxen puffat underifrån (tre observationer). När ungfågeln vunnit höjd och flykten stabiliserats har kolonimedlemmar fortsatt att cirkla runt ett tag innan svärmen tunnats ut. Samma cirklande gjordes runt den flygande attrappen. En observation gäller över artgränser: en tornseglare gjorde en stunds uppehåll i sin flyttning (2 sept.) och flög flera gånger an mot en utflugen hussvaleunge som tiggde intensivt där den nödlandat på en husgavel. – Vad vi vet, har puffanden underifrån aldrig observerats hos tättingar som inte heller behöver beteendet eftersom utflugna ungar kan mellanlanda i skydd och där matas (jfr hussvaleungen).

Det finns en påfallande likhet mellan tornseglares beteende mot ungfåglar och delfiners vårdgivande beteende. Därför tillämpar vi här samma uppdelning. ”Eskorterandet” av ungfåglar tolkas följaktligen som en *beredskap* från de vuxnas sida att ingripa, cirklandet runt nykomlingen och attrappen är tecken på *upphetsning* och puffar underifrån är *stöd*. Enligt vår tolkning har ett identiskt hot, att sjunka, drivit två mycket olika djurformer mot samma beteende.

Samma hot gäller unga sillgrisslor. Ungfåglarna hoppar från bohyllan i klippstupet och flyger ut mot havet innan de ens är halvvuxna. Ibland hamnar de i stenskravlet mellan klippstupet och strandkanten och blir där ett lätt byte för trutar och fjällrävar. Föräldrarna uppvisar ett tydligt vårdgivande beteende. Under utflygningen eskorterar de ungen. Det finns också seriösa rapporter om hur föräldrar antingen bär ungen i näbben mot vattnet eller puffar ungen underifrån flera gånger så att den når ut till vattnet. En sådan observation fick vi genom vårt upprop.

Vi känner till fyra publicerade observationer av vuxna tornseglares beteenden mot unga tornseglare, den första från 1939. Två senare publikationer rapporterar kontakt vinge mot vinge eller flygning tätt intill av vuxna. Det konstaterades också att de vuxna i de här fallen inte kunde vara föräldrar till ungfåglarna. Den fjärde observationen är även den lik vår egen där vuxna seglare kom ner till och ledsagade den unga fågeln. Beteendet betecknas som en ”välkomnande inspektion”.

En alternativ tolkning är att uppvaktningen är en aggressiv handling. I uppsatsen från 1939 beskrivs anflygningen som förföljelse och angrepp. Det är väl känt att skadade och sjuka djur med sitt avvikande beteende och individer med avvikande färg kan angripas av artfränder. Utflygande unga tornseglare flyger vingligt med ovana vingslag innan

flykten strax blir effektiv. Enligt den ”aggressiva” tolkningen skulle den osäkra flykten utlösa aggressionen.

I båda tolkningarna finns ett stort mått av subjektivitet. Trovärdigheten i den ena eller andra kan bara bedömas om detaljer i beteendet dokumenteras, t.ex. genom fotografiska belägg ”alive” och/eller med användning av attrapper. Vad man kan peka på är att ett luftburet kollektivt epimeletiskt beteende har observerats hos hussvalan som också den är anpassad för ett liv i luften. Puffar underifrån har setts hos alkor. Vi beskriver här också hur en ung tornseglare i skymningen spontant lämnar boet och utan rädsla (som det syntes) kastar sig ut mot koloniflocken som svärmar upphetsat utanför. Ungfåglar uppvaktas också efter att deras flykt stabiliserats. Till detta kan läggas att anflygningen mot den unga hussvalan av allt att döma inte var aggressiv. Vi finner med detta och parallellen med alkor att beteendet är epimeletiskt snarare än aggressivt och att den vårdgivande tolkningen har den största förmågan att förklara de olika beteendena.

En invändning mot uppkomsten av ett epimeletiskt beteende hos tornseglaren är att vuxna och ungfåglar aldrig möts i luften eftersom de vuxna redan vilar i boet när ungfåglarna flyger ut i skymningen. Vi konstaterar att beteendet finns och att det stereotypa draget tyder på en finjustering under lång tid.

Utflygande unga alkor eskorteras av sina föräldrar medan unga tornseglare uppvaktas av kollektivet och i vissa fall uppenbarligen av andra än föräldrarna. Är tornseglarnas beteende alltså exempel på oegennytta (altruism)? Det förs en omfattande diskussion om altruism förekommer hos djur eller inte. Enligt förhärskande teori innebär en hjälp till andra än den egna avkomman eller till nära släktingar alltid en förlust för givaren som i långa loppet gör att beteendet försvinner eller aldrig etableras. Man vet att tornseglaren inte känner igen sina egna ungar. Så länge tornseglaren var en relativt glest häckande urskogsfågel fick de egna ungarna automatiskt all omvårdnad. En hjälpaktion riktad mot en utflygande ungfågel gällde därför den egna avkomman och beteendet bör ha verkat för ett positivt urval. Vid uppkomsten av större kolonier minskade chansen att en ungfågel i nöd var den egna avkomman men beteendet bestod. Vi föreslår två huvudorsaker till detta: tornseglaren uppfattar varje utflygande unge som sin egen och är beredd att ”rädda” den samt att kostnaden för en räddningsaktion är försumbar i sammanhanget. Altruismen skulle m.a.o. vara missriktad ”egennytta”.

Appendix

Observations on the Common Murre *Uria aalge*
Location and date were the eastern side of Isle of Väröy, the next outermost island of the Lofoten island chain, Norway, at the July/August shift in 1972. The mountain at this part reaches 300 m a.s.l. and the cliffs with their ledges precipitate vertically to a slab stone shore, 50–75 m in width until the sea meets. On 4 or 5 August there was a common fly-out of young Murres, well anticipated by local residents who gathered on the shore to pick up and carry to the sea fledglings that fell on the stony shore. Often the young that fell among the stone rubble came off well and helped themselves to the sea and their waiting parents. However, of course some fell victims to hungry gulls. At three occasions, I could see how an adult Murre flew under the young and pushed it upwards one or two times so that it landed right out in the water. This was seen with field glasses (Zeiss 7x42) in a good afternoon and evening light during the prevailing period of midnight sun. I saw the birds very fine, obliquely from below and from the side. My position was on the rubble shore halfway between the seashore and the cliff where the birds nested. In spite of an active searching, I failed to find the Thick-billed Murre *U. lomvia.* Thus, all Murres seen were of the species *Uria aalge.* (Lars von Konow, answer 19 February 2008 to a national request)

How do the young alcids leave their nesting places? (Abbreviated from Swedish)
In the summer of 1910, I camped a few days (28–31 July) at Cape Diabas at the mouth of Sassen Bay (Isfjorden, Spetsbergen). During the fine nights when the sun stood at the cape, I used to keep at the near bird-mountain, taking photos and making observations. When sitting high up on the mountain and looking down toward the glassy water of the fjord, one sometimes saw a young auk [*Uria lomvia*] being piloted to the water. I was not in the position to see the preparation itself of the descent. First when the descent had started, could I observe and then follow it. By that, one of the parents and the young flung out from the mountain side, the adult with a firm hold by the bill over the back of the young. Whether the grip was over the back proper or at the base of the wing, I cannot settle now. When this happened, I was not aware that the question was not investigated and did not note in detail my observations which, however, stay very clear in my memory. In this grip, the young half hang, half waved its wings. The adult bird, with its neck stretched and head lowered, apparently and to a considerable part carried and steered its burden which itself seemed to contribute. The adult thus served as a sort of living parachute. Immediately after that they had plopped into the water, a diving and a fuss started, resembling a fight.
The distance to the water was in this case quite insignificant why the descent occurred rapidly and with a rather steep inclination. However, it is probable that a descent can be directed so that the drop occurs quite slowly and gradually, if needed. (Olofsson, Ossian - Fauna och Flora 1925, Vol. 20: 90–91.)