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Behaviour of Common Swift *Apus apus* and Western House Martin *Delichon urbicum* towards a flying dummy

Tornseglarens Apus apus *och hussvalans* Delichon urbicum *beteende gentemot en flygande attrapp*

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WE TESTED for airborne epimeletic (care-giving) behaviour in Common Swift *Apus apus* towards young swifts during their first flight. Tests were performed where colonies of Common Swift and Western House Martin *Delichon urbicum* co-occur. Three variants of a flying dummy were used; two with pointed wings of which one entirely black (1) and one with partly white body (2). The third was black with broad wings (3). Reactions were documented on film. Swifts and martins had opposite reactions to dummies 1 and 2. As we anticipated, martins seemed supportive in a test with dummy 2 and seemed to 'guide' the dummy epimeletically. However, a swift approached dummy 2 in a support-like attempt, but deviated after a close look. In a test with dummy 3, swifts acted highly hostilely. We discuss reasons for these outcomes and the importance of dummy appearance. We illustrate the flight paths of the dummy, swifts and martins with trajectories, and the behaviour of the Western House Martin is shown in stepwise larger magnification stills of a video.

Keywords: epimeletic behaviour | care-giving behaviour | flight trajectory | offspring recognition | wing shape | Apodidae | Hirundinidae

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Introduction

Birds, like vertebrates in general, invest a great amount of energy in feeding and care for their young. In comparison, a rescue action for young in peril may be cheap, even in the case of seemly altruistic support directed toward a non-relative. The background to this study is two such observations of airborne supporting behaviour, i.e., an *epimeletic* (Greek: caregiving) behaviour in the social life of Common Swift *Apus apus* (Tenow *et al.* 2008).

The first observation was made on 17 July 1979, when a full-grown fledging was found on the ground. When launched into the air by one of us (OT), it was immediately caught up from behind by an adult swift, which seemingly touched the fledgling from below until the young flew safe together with members of the colony.

The behaviour observed in this case did not seem to be an isolated phenomenon. The second observation occurred on a day in the shift between July and August 2006 at a house on the southern part of the island Öland, about 300 km south of the former observation. A full-grown fledgling was found on the ground and tossed in the air. Immediately, two adults approached the young. In this case, it was seen very clearly that the young swift was pushed repeatedly from below by one of the adults until it flew with ease, circling together with adults of the colony (observation by Stefan Asker).

Based on the two observations described above, we hypothesized that Common Swifts give airborne support to fledglings that risk to fail their first flight, often called 'maiden flight'. This is crucial because if the young swift falls to the ground, it cannot get back into the air again. We wanted to test this hypothesis by confronting adult swifts with two variants of a flying dummy, one with pointed wings and one with broad wings, and record their reaction on film. We also tested the hypothesis that another air-bound species, the Western House Martin *Delichon urbicum,* may have evolved an epimeletic behaviour similar to that of swifts (Tenow *et al.* 2008).

In this paper we interpret behaviour according to the scheme by Caldwell & Caldwell (1966), created for cetaceans such as dolphins (cf. Tenow *et al.* 2008). The reason is that both cetaceans and swifts live in non-supporting elements (water and air). Epimeletic behaviour is divided in two categories: one, *nurturant*, where care is directed towards young, and one, *succorant*, where care is directed from adult to an adult. In the latter category, behaviour is divided into three grades of increasing intensity: (1) 'standing by', (2) 'excitement' and (3) 'support', e.g. pushing a dolphin from below that risks drowning or a swift at risk of falling to the ground. Nurturant is here used for behaviour directed toward young that cannot feed themselves. Consequently, succorant is behaviour directed towards individuals that feed independently, and since fledged swifts do so, we therefore treat them here as adults.

Material and methods

COMMON SWIFT AND WESTERN HOUSE MARTIN

Few birds of other bird families are as visible, and still enigmatic, as the Common Swift when it flies both high and low in the summer sky over towns and on the countryside. Its behaviour and extreme adaption to an airborne life has long attracted and fascinated researchers. Much has been learned in recent time about the life of swifts, such as their migration routes to and from their breeding sites (for an overview, see Åkesson *et al.* 2012). Different airborne behaviours have been described, such as swifts collectively ascending high up in the sky at dusk (Nilsson *et al.* 2019). With Tigges (1999) finding of territory-holding by colony members, he answered the question of why 'screaming parties' are observed. With this behaviour, they claim of ownership of the colony territory (Tigges 1999).

Western House Martins are also highly visible when they fly in large numbers in rural and urban areas, snapping insects in the air. Although not as extremely adapted as swifts to an airborne life, they have a much higher flight ability compared to most other passerines (Rosén *et al.* 2007). When needed, for example when collecting mud pellets for nest building, they will land and take off from the ground. Like swifts, martins are highly social birds that breed in colonies.

Common Swifts and Western House Martins sit on evolutionarily deeply separated phylogenetic branches, belonging to orders Apodiformes and Passeriformes, respectively (Ericson 2008). Despite that both species are adapted to an airborne life as feeders of aerial prey, they are morphologically different, particularly in the structure of the wings. In passerines, to which the Western House Martin belongs, the different wing bones are of about the same length, whereas in swifts

FIGURE 1. (**a**) Common Swifts *Apus apus* of the swift colony in this study joined in a "screaming party" of about 25 birds. (**b**) Screaming party meeting dummy (far right) with pointed wings. Photo: MWP.
— (***a***) *Tornseglare* Apus apus *av den studerade tornseglarkolonin i högljutt kretsande (s.k. "screaming party") runt sitt boställe i ett sommarhus.* (***b***) *Ett högljutt sällskap möter den spetsvingade attrappen (längst till höger). Foto: MWP.*

the end phalanx is much prolonged (Chantler 2000), which renders the swift wings their typical crescent-like shape (Figure 1a). The structure also affects the way of flight (Gustafson & Lindkvist 1985), powerful in swifts, but in martins somewhat fluttering with wings intermittently folded backwards. The Common Swift also has a larger wingspan than the Western House Martin. Swift fledglings feed themselves from the start, while martin fledglings learn to do so gradually.

STUDY SITE

The study site, the house 'Rian' and surrounding area, is located on the grounds of Frösåker estate, Västerås Municipality, north of Lake Mälaren, central Sweden (59°32′ N, 16°44′ E). Rian was the site for the first observation (above) of an airborne supporting behaviour in the Common Swift. For an aerial photo of the site, see Tenow *et al.* (2008). At the site there is a small breeding colony of swifts, with 5–9 pairs distributed over three nearby buildings, plus single pairs breeding in natural holes in trees. Including non-breeders, the colony often numbers more than 20 swifts (Figure 1).

In the vicinity, there is also a colony of Western House Martins distributed under the eaves of a former mill with an annexed sawmill just to the south-east, and on a large barn about 200 m to the east. For a photographic overview, see Figure 1 of Tenow *et al.* (2008).

DUMMY FLIGHTS

Two specimens of the commercial toy Bionic Bird (Edwin van Ruymbeke, Marseille, France) were used to entice reactions. In the first, the wing area was reduced

FIGURE 2. The two variants of dummies used in the tests. (**a**) The reshaped dummy with pointed wings. (**b**) The original Bionic Bird with broad wings. *— De två varianterna av attrappen som användes vid testerna. (**a**) Den omskapade attrappen med spetsiga vingar. (**b**) Bionic Bird-originalet med breda vingar.*

to give the wings a pointed shape in order to be more swift-like (Figure 2a), whereas wings were kept in the original broad shape in the second one (Figure 2b). The Bionic Bird is black with black wings (like a Common Swift) but on the first dummy, when worn, the white base colour on the sides of the body became visible. Body length of the dummy was 16 cm, wingspan 33 cm and weight 9 g. For comparison, the same measurements for Western House Martins are 12 cm, 26–29 cm and 15–23 g, and for Common Swifts 17–18 cm, 40–44 cm and 40–45 g (Mullarney *et al.* 1999).

The speed (via wing beat frequency) and direction of flight was regulated with an app in a smart phone. During dummy flights, wing beat frequency was mostly kept at its maximum (18 Hz). When the wing area (2.7 dm^2) was reduced, as with the pointed wings, beat frequency was increased to maintain speed.

The maximum distance to maintain contact with the dummy is 100 m. If the dummy consistently deviated to the left or right, the flight direction was adjusted by putting a smaller or larger piece of aluminium tape on the tip of the opposite wing until the dummy flied correctly in a balanced manner. Wing flapping is driven by an electric motor, furnished by an on-board chargeable lithium battery.

To test the hypothesis that adult Common Swifts support fledglings that risk to fail during their first flight, the two types of dummies were released from the hands of the operator of the smartphone. Observations were made in an open area with as much free sight as possible and recorded on video.

RECORDINGS

Documenting Common Swift behaviour depends much on equipment and chance: a well-balanced dummy handled correctly, a day with fine weather and weak winds, Common Swift presence, and a photographer on the spot. Getting this together at the study site was possible during four of the six summers of the study.

The first use of the Bionic Bird was in 2015, then with the original broad-winged dummy. In 2016, the dummy with pointed wings was introduced. During days with opportunities to document behaviour, several videos were obtained per day, in total 25 videos during six days in 2016. A majority of the 25 videos show Common Swifts and Western House Martins approaching the dummy. In two cases the species approaching is uncertain. In six cases the dummy failed because it deviated to the ground, and in six cases no swifts showed up.

TABLE 1. Main video recordings of the study. Dummy operator: OT.
– Huvudsakliga filminspelningar som diskuteras i studien. Attrappen kördes av OT.

Film (file) *Film (fil)*	Dummy *Attrapp*	Species interacting *Interagerande art*	Date and photo *Datum och foto*	Video length (time analyzed) *Videolängd (analyserad tid)*	Filming equipment *Filmutrustning*
Film 1 (file 1, Supporting information)	#1: Pointed wings, black *#1: Spetsiga vingar, svart*	Common Swift *Apus apus tornseglare*	25 June *juni* 2016, Ragnar Malmborg	40 s (40 s)	Apple iPad Pro (9.7 inches, 2015–2016) with a frame rate of 30 frames (pictures or stills) per second. *Apple iPad Pro (9,7 inches, 2015–2016) med bildfrekvens om 30 rutor (bilder) per sekund.*
Film 2 (files 2–3, Supporting information)	#2: Pointed wings, black and white *#2: Spetsiga vingar, svartvit*	Western House Martin *Delichon urbicum hussvala*	22 July *juli* 2016, Marcus Malmborg	68 s (22 s at 43–64 s; 44 s included in file SD2) and 3-second loop (SD3)	Same Apple iPad Pro as film 1 above. *Samma Apple iPad Pro som film 1 ovan.*
Film 3 (file 4, Supporting information)	#2: Pointed wings, black and white *#2: Spetsiga vingar, svartvit*	Common Swift *Apus apus tornseglare*	17 July *juli* 2020, MWP	13 s (13 s)	Canon 7D mark II camera equipped with a Canon EF 100–400 mm 1:4.5–5.6 lens. Speed 25 frames/sec, resolution 1 920×1 080 dpi. A tripod with a monoball tripod head was used for stability. *Kamera Canon 7D mark II utrustad med objektiv Canon EF 100–400 mm 1:4,5–5,6. Bildfrekvens 25 rutor/s, upplösning 1 920× 1 080 dpi. Ett stativ med kulledshuvud användes för stabilitet.*
Film 4 (file 5, Supporting information)	#3: Broad wings, black *#3: Breda vingar, svart*	Common Swift *Apus apus tornseglare*	4 August *augusti* 2015, Ragnar Malmborg	47 s (47 s)	Same Apple iPad Pro as film 1. *Samma Apple iPad Pro som film 1.*

In the summers of 2017 and 2020, two videos and one film (by MWP) with a highspeed camera were recorded. In addition, one film was obtained with a highspeed camera in 2017 by Andrzej Markiewicz (Discussion). All recordings were obtained at the study site Rian (above). The four recordings (Table 1) are numbered in the order they are treated in Results and the Discussion.

TRAJECTORIES

Trajectories were created from films 1 and 2, using the technique of iskiography (Schiffler 2018). Unlike a photographic long-term exposure of moving lights at night, the results here are not bright lines of light, but the motion-tracks of dark objects against a bright background. In this process, a video is first split into up to thousands of single images, which are then superimposed again into one

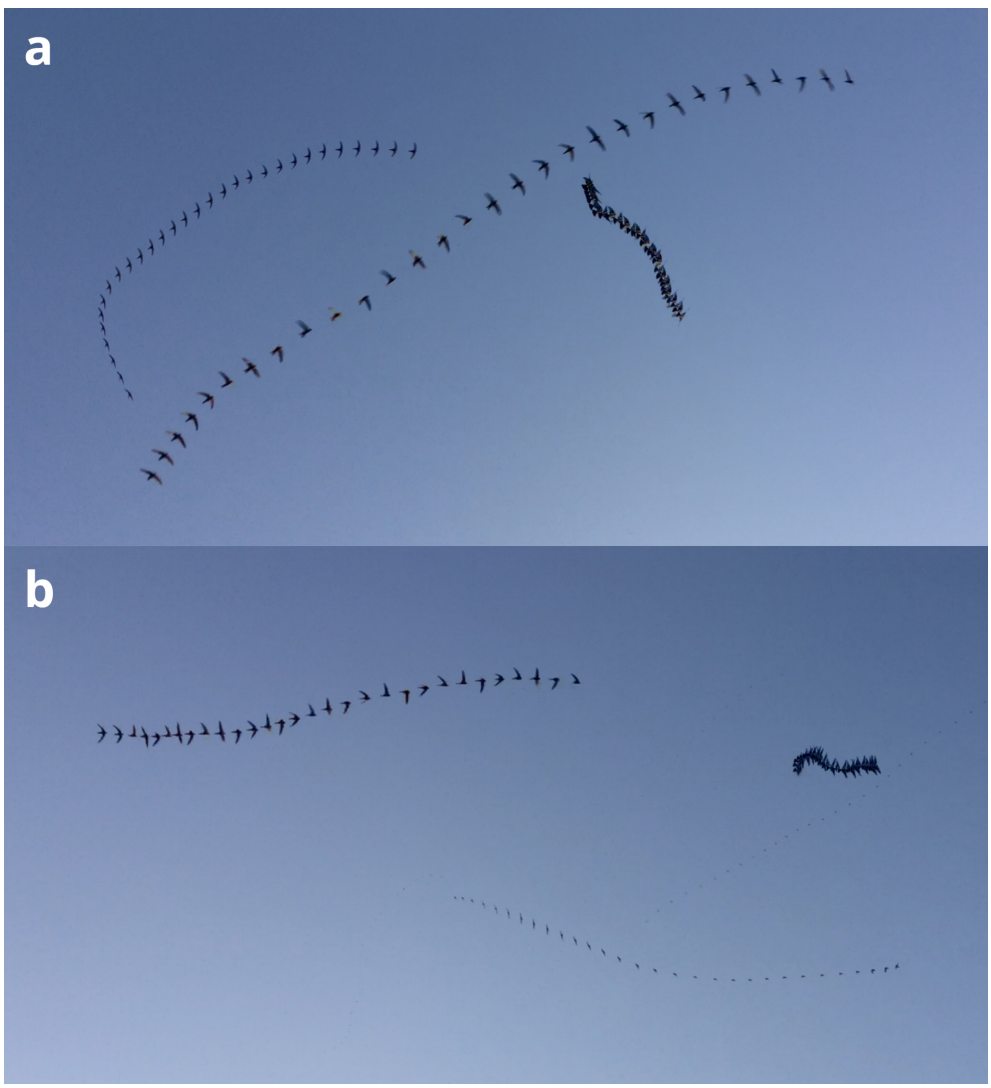

FIGURE 3. (**a**) Common Swifts *Apus apus* circle around the pointed winged dummy, see text. Clip 1 from film 1. (**b**) A Common Swift approaches the pointed winged dummy, see text. Clip 2 from film 1. In both stills, the darker trajectory is from the dummy. Film 1 is available as Supporting information. — (***a***) *Tornseglare* Apus apus *cirklar runt den spetsvingade attrappen (se text). Klipp 1 från film 1.* (***b***) *En tornseglare nalkas den spetsvingade attrappen. Klipp 2 från film 1. I båda stillbilderna är den mörkare banan från attrappen. Film 1 är tillgänglig som supplement 1.*

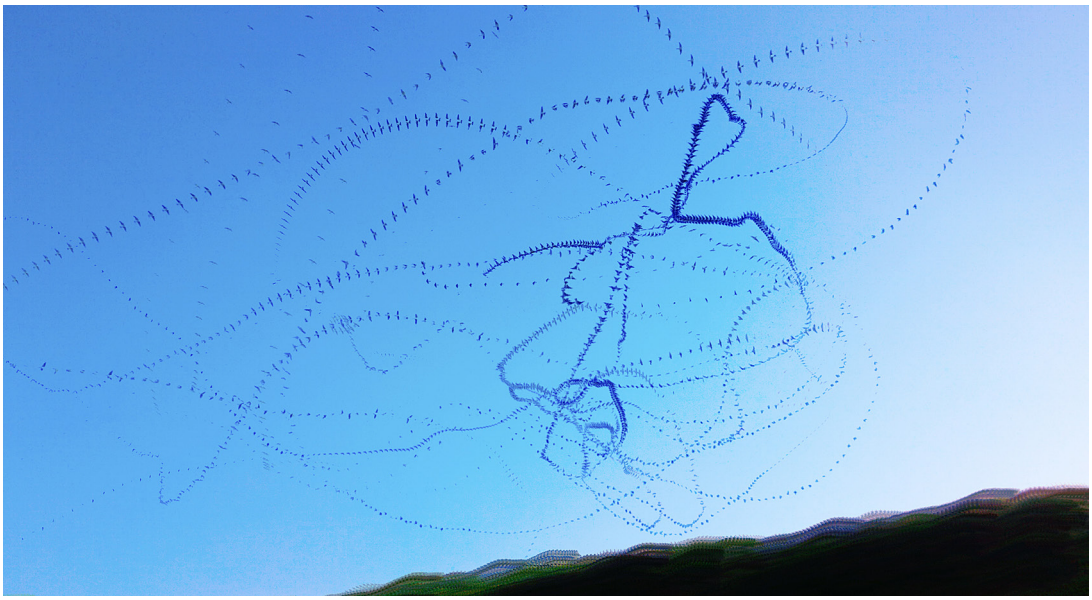

FIGURE 4. Trajectories of 4–5 Western House Martins *Delichon urbicum* (birds with white underside) gathering around the dummy with pointed wings (darker trajectories). In this summary over time from second 43 to second 64 the later part of film 2, which lasted 68 s in total, the dummy has made two loops, one high up and one low down. They appear compact dark because of the broad wing base of the dummy and the lower flight speed/higher wing beat frequency of the dummy compared to that of the martins.
— Banor för 4–5 hussvalor Delichon urbicum *(med vit undersida) som kretsar kring attrappen med spetsiga vingar (mörkare spår). Bilden är en summering över tiden (från sekund 43 till sekund 64 av den senare delen av film 2, som varar 68 sekunder totalt) av banor för hussvalor och attrapp där attrappen gjort två slingor, en högt upp och en lågt ner. De framstår kompakt mörka pga. attrappens breda vingbaser och dess låga flyghastighet/höga vingslagsfrekvens jämfört med hussvalors.*

image by means of an algorithm (Schiffler 2018). Here, this method is used to track the movements of the dummy, the martins, and the swifts. In a first step, 22 trajectories were created, each one out of 30 stills from film 2 and thus representing one second each. These partial trajectories were then combined into one still image now showing a period of 22 s of the video (under Observation 2).

Since the iskiographies processed on the basis of film 2 represent a combination of bird flight and camera panning it is difficult to identify the actual movements from the trajectories. In order to create an iskiography which solely reproduces the trajectories of martins and dummy, it would be important for the camera to be firmly mounted on a tripod during recording.

Results

OBSERVATION 1

We observed swifts approaching and circling around the dummy with pointed wings seemingly in an eager, agitated manner, however without touching it (film 1, Supporting information). A still from the film (Figure 3) shows (during second 28 from the start of the film) how a Common Swift approaches the dummy from behind before it deviates from the dummy.

OBSERVATION 2

We also observed a Western House Martin 'guiding' the dummy in the way described by Lind (1960). The approach to the dummy, shown in the film 2 (file 2, Supporting information) and an extracted 3-second sequence (file 3, Supporting information), is here presented in three successive steps (Figure 4–6), showing the movements of the martin and dummy in still greater detail. In its total length, the film lasts 68 s (Table 1). It shows the movements of the dummy and martins (and to a certain extent that of the camera), summed over a timespan of 22 s (caption) of the film with movements visualized by trajectories. Over the surveyed time, the dummy is tracked through two loops: one early, high up in the image, and one later, lower down; during both

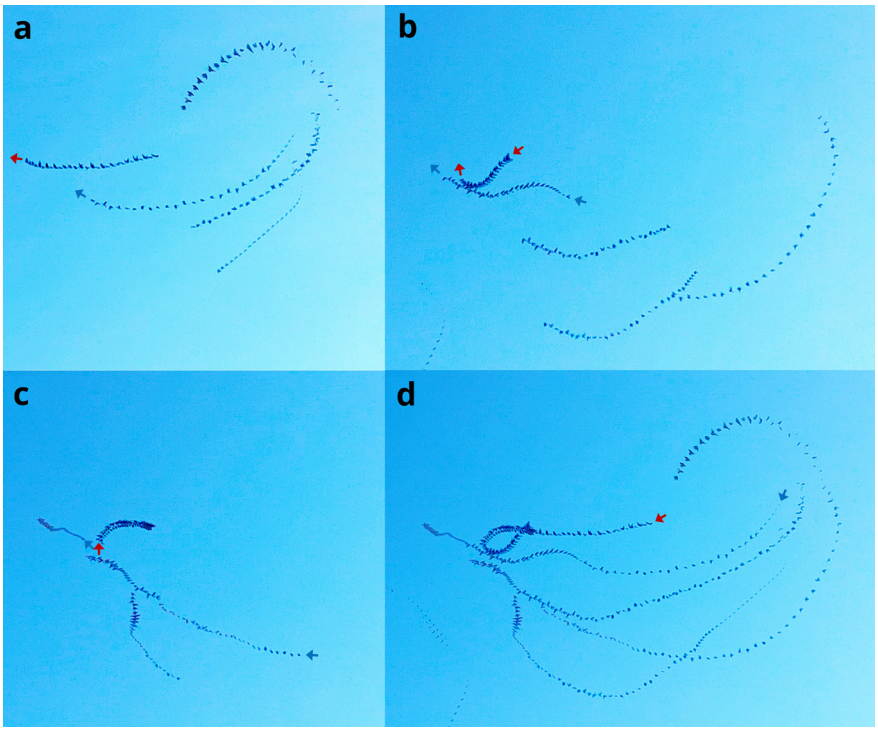

FIGURE 5. Magnification of the lower loop in Figure 4, showing (**a**) a Western House Martin *Delichon urbicum* (blue arrow) approaching the dummy with pointed wings (red arrow) and (**b**) passing under the dummy in a support-like behaviour. They then (**c**) separate and the dummy deviates upwards/backwards. The flight paths are visualized by trajectories of 1 s flight each: seconds 55, 58, and 59 (a–c) after the start of film 2, which lasts 68 s in total. The summary over time (**d**) corresponds to the centre of the loop in Figure 4. Trajectories are lighter for the Western House Martins and thick and dark for the dummy (also identified by the red arrow).
*— Förstoring av den undre slingan i figur 4. Den visar (**a**) hur en hussvala* Delichon urbicum *(blå pil) närmar sig attrappen med spetsiga vingar (röd pil) och (**b**) passerar under attrappen i ett stödliknande beteende. Därefter (**c**) skiljs de åt genom att attrappen avviker uppåt/bakåt. Flygväg visas med flygbanor om 1 sekund vid 55, 58 och 59 sekunder (a–c) från start av film 2, vilken varade 68 sekunder totalt. En summering över tid (**d**) återfinns i centrum av slingan i figur 4. Flygbanorna är ljusa för hussvalan och mörkare för attrappen.*

surrounded by martins (with white undersides). Both started by a Western House Martin catching up with the dummy that then rose steeply. In the first case, the martin came from the left and below (however, not as close as in the lower loop) in second 47 from the start of the video. This means that the upper loop occurred at the start of the 22 s compounded in Figure 4 (details not shown, cf. Figure 4).

In three extracts from the later part of the film 2 (Supporting information), it appears that the Western House Martin (Figure 5a–c) approaches, catches up with (cf. Figure 6) and separates from the dummy, each shown with trajectories. It is also evident that three martins follow the dummy/martin couple. This short passage, summed up in Figure 5d, occurs in the centre of the lower loop of Figure 4, later in time. After this, the dummy and the Western House Martin both rise (the dummy more steeply).

Figure 6 shows in eight picture frames, enlarged and in detail, the 'catch-up', seen in Figure 5b. The images are blurry but interpretable. These images and the film clip (file 3, Supporting information), show that the Western House Martin, when catching up with the dummy from behind, raises its body upwards to gain height while clearly targeting the dummy from below (Figure 6a–c). At the same time, it synchronizes its wing beats with those of the dummy (Figure 6d–e). They thereafter both fly horizontally, the martin below the dummy, although without touching (Figure 6e–f). Finally the martin flies in front of the dummy (Figure 6g–h) until they separate, mainly by the dummy rising steeply (Figure 6h). The different phases in this paired flight are summed up in

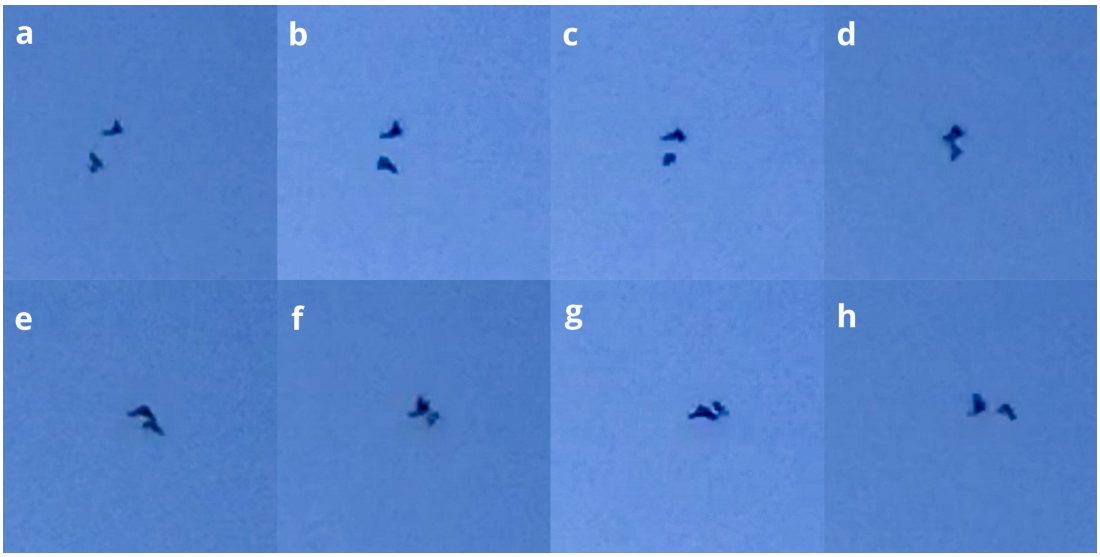

FIGURE 6. Magnification of part of Figure 5b, mirrored horizontally so the sequence can be read from left to right (a–h), showing support-like behaviour of a Western House Martin *Delichon urbicum* directed towards the dummy with pointed wings. All eight phases, described in Table 2, occurred within 1 s. From film 2 (Supporting information, files 2–3).
— Förstoring av en del av figur 5b, spegelvänd horisontellt så att den kan läsas från vänster till höger (a–h), vilken visar ett stödliknande beteende av en hussvala Delichon urbicum *riktat mot attrappen med spetsiga vingar. Samtliga åtta faser, beskrivna i tabell 2, inträffade inom 1 sekund. Från film 2 (supplement 2–3).*

Table 2. All eight phases together occur within second 58 of the 68-second-long video.

OBSERVATION 3

In film 3 (file 4, Supporting information), a Common Swift and the dummy with pointed wings are seen in the same vertical plane from the rear end. It shows how the swift descends from the sky and approaches the dummy from behind and below. This is also seen in six stills from the later part of the film (Figure 7 a–f).

OBSERVATION 4

Stills from film 4 (Figure 8, Supporting information) are used here to illustrate the large difference between the behaviour of swifts towards the dummy with broad wings and the variant with pointed wings (Observation 3 above).

The stills (Figure 8a–c) show how the broad-winged dummy flies and how three Common Swifts, one after the other, descends from the sky, each in a dive, targeting the dummy and then after a sharp turn, returns to the sky. The first swift dived within 1 s and all swifts within 7 s from the release of the dummy. When the dummy reached the sky, swifts there made similar rapid dives that targeted the dummy (film 4, Supporting information).

Discussion

Based on two previous observations, referred to in Tenow *et al.* (2008), we hypothesized that an epimeletic (care-giving) behaviour exists where adult Common Swifts support young swifts in their flight debut. We suggested that also the Western House Martin could have evolved similar behaviour. Our aim was to document on film that Common Swifts may support young swifts from below during their first flight. During this study we also observed and documented possible epimeletic behaviour in the Western House Martin.

EPIMELETIC (CARE-GIVING) BEHAVIOUR

We tested whether we could elicit epimeletic behaviour in swifts and martins using a flying dummy bird and recording behaviours with digital cameras. Over the course of three summers, we observed such behaviours in two instances. In the first, a Western House Martin responded support-like to the dummy with pointed

TABLE 2. Comments to Figure 6a–h, from film 2 (Supporting information).
— Kommentarer till figur 6a–h, från film 2 (supplement 2–3).

Panel	Actor *Aktör*	Wing position *Vingposition*	Behaviour *Beteende*	Synchronization *Synkronisering*
6a	dummy *attrapp*	upward *uppåt*	horizontal flight *horisontell flykt*	
	martin *svala*	upward *uppåt*	rising, targets the dummy from behind and below *stigande, tar sikte på attrappen bakifrån och underifrån*	
6b	dummy *attrapp*	upward *uppåt*	horizontal flight *horisontell flykt*	
	martin *svala*	downward *nedåt*	raising, targets the dummy from behind and below *stigande, tar sikte på attrappen bakifrån och underifrån*	
6c	dummy *attrapp*	downward *nedåt*	horizontal flight *horisontell flykt*	
	martin *svala*	midway? *halvvägs?*	rising, right under the dummy *stigande, omedelbart under attrappen*	start of synchronization *synkronisering startar*
6d	dummy *attrapp*	upward, midway *uppåt, halvvägs*	horizontal flight *horisontell flykt*	
	martin *svala*	upward *uppåt*	rising, flight under the dummy *stigande, flykt under attrappen*	synchronized *synkroniserade*
6e	dummy *attrapp*	downward *nedåt*	horizontal flight *horisontell flykt*	
	martin *svala*	downward *nedåt*	horizontal flight, below and a little forward of the dummy *horisontell flykt, under och något framför attrappen*	synchronized *synkroniserade*
6f	dummy *attrapp*	upward *uppåt*	horizontal flight *horisontell flykt*	
	martin *svala*	upward, midway? *uppåt, halvvägs?*	horizontal flight, halfway in front of the dummy *horisontell flykt, under och något framför attrappen*	end of synchronization *synkronisering slutar*
6g	dummy *attrapp*	downward *nedåt*	horizontal flight *horisontell flykt*	
	martin *svala*	upward *uppåt*	horizontal flight, in front of and level with the dummy (guiding) *horisontell flykt, framför och i höjd med attrappen (vägleder)*	
6h	dummy *attrapp*	upward *uppåt*	rising *stigande*	
	martin *svala*	downward *nedåt*	horizontal flight, in front of and level with the dummy (guiding) *horisontell flykt, framför och i höjd med attrappen (vägleder)*	

wings (Figure 5a–c, file 2, Supporting information). The stills in Figure 6 (film in file 3, Supporting information) show how a martin catches up with the dummy from behind and below, and passes tight under it with wing beats synchronized with those of the dummy before they separate. In the second instance, a Common Swift shows a similar approach from behind the dummy with pointed wings (Figure 7, file 4, Supporting information). The behaviour of the martin and the swift in these two cases may fall under the epimeletic concept. However, the swift behaviour of circling around the dummy with pointed wings, and approaching it from behind in film 1 (Supporting information, Figure 3), was probably more from curiosity than for any other reason.

In film 2 (Supporting information) and Figure 6, the Western House Martin passes tightly under the dummy but does not touch it. Thereafter, the dummy rears upward and backward. This is seen twice in film 2, one in the first half of the film sequence (not shown in detail) and one in the second half (Figure 4–6). In the first case, a martin is coming from the left, targets the dummy from below and behind when the dummy rears upward and backward, forming the upper loop. In the second case, the martin is close to the dummy, just in front of it, when the dummy rears backward, causing the lower loop.

From the description above, it may look like the Western House Martin trying to support the dummy from below, as observed for Common Swift. However, the epimeletic behaviour of adult martins and swifts are, out of necessity, fundamentally different: a young swift must be able to fly immediately when it leaves the nest and thereafter feed itself, while a young martin, being a passerine, gradually learns to fly effectively. At its first flight, the young Western House Martin always leaves the nest together with, and behind, one of its parents (Lind 1960). This order, with the parent first, is described by Lind (1960) as 'guiding', i.e., an adult shows the young, that follows closely, the way of flying. The first flight may sometimes lead back to the nest, where the young may even stay overnight (Lind 1960). Once fully fledged, it can perch away from the nest and receive food from its parents (Tenow *et al.* 2009).

In our test, the dummy that stood in as a 'young bird', was already on its wings alone, so the Western House Martins had to catch up with it. The fastest and most effective way to do that and then lead it, is to approach from behind, pass under it with wing beats synchronized to those of the dummy, rise in front of it, and then guide the dummy.

Lind (1960), in his detailed study of the behaviour of Western House Martin, importantly does not mention that adults may pass under and support the young from below. The reason for this is the absence of need for such support: if a young falls onto the ground but is unharmed, it should be able to take off again. Accordingly, the epimeletic behaviour of House Martin seen here might fall under the category *nurturant*. For a nurturant behaviour of Common Swift, directed toward a young, perching Western House Martin, see Figure 1 of Tenow *et al.* (2009). We find some support for the hypothesis that the Western House Martin has evolved an epimeletic behaviour that is specific for an aerially feeding passerine species.

It is interesting to note that both Western House Martins and Common Swifts targeted a non-relative, the dummy, thus showing an indiscriminative behaviour. For the swifts, a possible background to such a behaviour may be sought in the history of the species. Before humans occupied the land, Common Swifts lived in forested areas and bred in tall trees in abandoned hollows originally made by woodpeckers (Günther & Hellmann 2004), or in crevices in cliff sides. At that time, with a sparsely distributed population, a young swift making its first flight was likely the offspring of the two adults flying in the area (Tenow *et al.* 2008). Later, human exploitation resulted in many buildings with an abundance of cavities suitable for nesting places. No longer limited by access to nesting places, swift populations increased strongly (Tenow *et al.* 2008). In this new situation, parents might not recognize their own fledged young birds (below).

Common Swift parents accept nestlings from other nests and care for them *alloparentally* as their own (Hahn & Yosef 2020), which is also an epimeletic behaviour. Hypothetically, this implies that swifts do not discriminate between their own fledged offspring and others. An indication of that in our tests is that a swift seemed to support the dummy with pointed wings (Table 1, Figure 3, file 1, Supporting information). In the observation by Tenow *et al.* (2008; see Introduction) the intervening adult could not have been a parent of the released young swift. This behaviour should be classified as 'standing by' under the category succorant behaviour.

Close approaches to young swifts during their first flight by adults have been interpreted by some as aggression (Goethe 1939). We argue that rather than

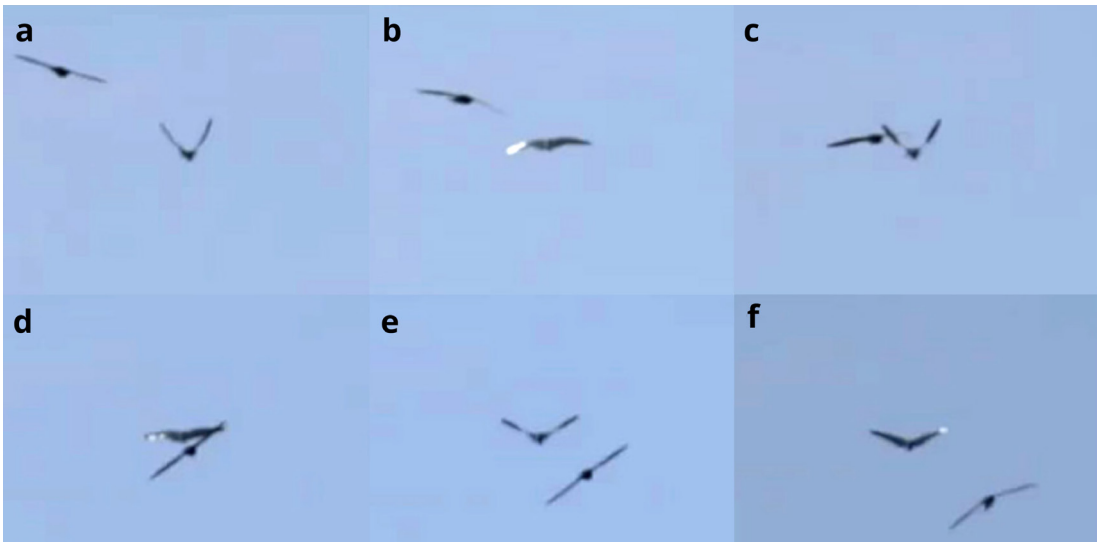

FIGURE 7. Support-like behaviour of a Common Swift *Apus apus* towards the dummy with pointed wings when catching up with it. Within second 6 in sequences of film 3, clip 2, the swift (**a–c**) gradually approaches the dummy (which is at the center of the images) from behind until it (**d**) seemingly is under the dummy, twitches, and then (**e–f**) separates from the dummy.
— Stödliknande beteende av en tornseglare Apus apus *mot attrappen med spetsiga vingar när den flyger ifatt attrappen. Inom sekund 6 av film 3, klipp 2, (**a–c**), nalkar tornseglaren attrappen (som är i mitten av bilderna) bakifrån tills den (**d**) till synes är under attrappen, rycker till, för att sedan (**e–f**) avvika från attrappen.*

aggression, it should be seen as a strong urge to 'stand by' and to 'support', falling within the succorant category (Caldwell & Caldwell 1966). In contrast, an aggressive attitude is expressed as rapid dives as towards an enemy as seen in film 4 (file 5, Supporting information).

Lind (1960) offers a detailed description on the behaviour of adult Western House Martins vis-à-vis their offspring. When nestlings are placed in another nest with young, the adults there feed them as their own. However, as grown and fledged, the parents feed only their own fledged young.

In both species, the first flight of fledglings is an important occasion that engages colony members. When Western House Martins loudly encourage their young ready to fly out from the nest, colony members join and assist in the encouragement. When the young leave the nest, one of the parents gives airborne care by guiding the flight of the young, which follows tightly behind. Sometimes, the parent leads the flight back to the nest (Lind 1960). A similar excitement occurred at the study site when a young Common Swift flung itself

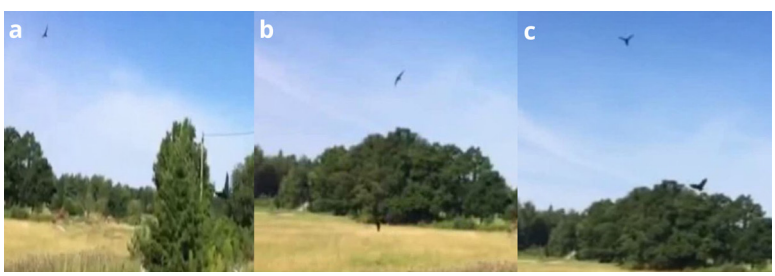

FIGURE 8. (**a–c**) Turning points of dives of three Common Swifts *Apus apus*, one after the other diving towards the broad-winged dummy within 7 s. The dummy can be seen (**a**) to the right of the telephone pole, (**b**) at the border between the oak grove and the field, and (**c**) at the border between the oak grove and the sky. From film 4 sequences (file 5, Supporting information).
*— (**a–c**) Vändpunkten för tre tornseglares* Apus apus *dykningar, en efter en, mot den bredvingade attrappen, alla inom sju sekunder. Attrappen syns (**a**) till höger om telefonstolpen, (**b**) på gränsen mellan ekdungen och fältet, samt (**c**) på gränsen mellan ekdungen och himlen. Från sekvenser ur film 4, supplement 5.*

out of the nest in front of a large number of colony members, which then escorted it (Tenow *et al.* 2008).

RECOGNITION OF CONSPECIFICS

When adults initiate a rescue action, they must have recognized the young in need of help. Birds that are ground-dwellers or live in dense vegetation, and airborne birds like swifts, use very different signals to discriminate their fledged young from those of others. Among the former, the contact between parents and their fledged young is still intense. For the fast-flying swifts, a young bird must be rapidly recognized through distinct signals, not as individuals but as conspecifics. We suggest that, most probably, those signals are the unique crescent-shaped and sharply pointed wings, and the blackish body.

Supporting this, and demonstrating interesting behavioural differences from Western House Martins, is our observation that the entirely black dummy with pointed wings, strongly attracted Common Swifts in early summer (film 1), while martins stayed away. One month later, when the black surface of the dummy's white base was partly worn off, giving it contrasting white and black parts of the body, the behaviour was reversed and the dummy attracted martins (film 2) but not swifts. Similarly, in a still (Figure 1b) from film 3 when the dummy was worn, a screaming party of swifts met the dummy without any reaction despite its pointed wings.

The behaviour of swifts differed also when they encountered the dummy with pointed wings versus the dummy with broad wings, suggesting that the wing shape is important. One can compare the approach of the Common Swift towards the dummy with pointed wings in the six stills from film 3 (Figure 7) with the behaviour of swifts exposed to the dummy with broad wings in film 4 (Figure 8). In the first case the swift glides down gently, mostly with wings held horizontally when it catches up with the dummy from below, before they separate. This seems non-aggressive. Likewise, a non-aggressive behaviour of swifts circling around and catching up with the dummy with pointed wings is documented in Figure 3 (from film 1). In contrast, the sharp dives towards the dummy with broad wings are decidedly hostile and there is no following or circling around it (Figure 8, film 4) and the same behaviour is repeated high up in the sky (film 4). The dives near the ground clearly target the dummy, excluding the possibility that the dives would have been aimed at the operator of the dummy.

Presumably from the white on the worn dummy and other signals, the Western House Martins seen in film 2 perceived the dummy as a young conspecific in need of guiding. On the other hand, the same signals left the Common Swifts neutral. The swift in film 3 that approached the dummy with pointed wings came from above and may not have seen the white sides of the dummy until it was under it, which may even explain the stagger of the swift as seen in Figure 7d. Probably, the broad-winged, dark-coloured dummy was believed to be a corvid, which could be considered an enemy. Several corvid species are abundant in the study area. On one occasion (4 August 2017), a dummy with pointed wings went down in the open field at the study site. It kept fluttering, which immediately attracted several Eurasian Magpies *Pica pica*, Western Jackdaws *Coloeus monedula*, and Hooded Crows *Corvus cornix*. Parts of the event was filmed with a highspeed camera (by Andrzej Markiewicz; film not shown). The place itself and the loud quarrelling at the fluttering dummy were blocked by vegetation, but it seems that corvids are deadly threats to downed young swifts and other birds unable to fly.

Conclusions

Previously, at two occasions, adult Common Swifts had been observed to give airborne support to fledglings during their first flight (Tenow *et al.* 2008). With the present study, using flying dummies and photographic documentation, we offer further indirect support for the hypothesis of an airborne epimeletic (care-giving) behaviour in two aerial bird species, the Western House Martin (Hirundinidae) and the Common Swift (Apodidae). We also conclude that the epimeletic behaviour in the Western House Martin falls within the nurturant category epimeletic behaviours. Common Swifts and Western House Martins reacted differently to the dummy's wing shape and whether its body was entirely black or black and white.

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SUPPORTING INFORMATION

File 1: film 1; file 2: film 2; file 3: three-second sequence extracted and looped from film 2; file 4: film 3, clip 2; file 5: film 4. All supporting information is available at https://doi.org/10.34080/os.v34.23182.

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Svensk sammanfattning

BAKGRUND

I en artikel i *Ornis Svecica* rapporterade Tenow m. fl. (2008) två observationer av att flygande, vuxna tornseglare *Apus apus* med puffar underifrån kan hjälpa ungfåglar att inte förlora höjd under deras första, osäkra flygning. En utflugen ung tornseglare kan inte som andra ungfåglar slå sig ner på en trädgren och där bli matad av föräldrarna. Den måste under sin första flygning ta sig upp i luften. Faller den till marken, faller den snart också offer för luft- eller markfiender. För detaljer här och i det följande, se Tenow m. fl. (2008). I en andra artikel rapporteras hur en tornseglare, under givna betingelser, svarade positivt på tiggande läten från en utflugen hussvaleunge *Delichon urbicum* (Tenow m. fl. 2009). Föreliggande artikel är en uppföljning av dessa två rapporter.

INLEDNING

De två observationer som nämns ovan var skilda i tid och rum men annars mycket lika. Den första gjordes 17 juli 1979 vid Frösåker strax norr om Mälaren mellan Västerås och Enköping, Västmanlands län, den andra omkring juli–augusti 2006 eller 2007 på Alvaret, södra Öland omkring 300 km söder on den första. I båda fallen hittades en flygg ungfågel på marken under sin boplats under taket på en sommarstuga och kastades upp i luften. I båda fallen flög en eller ett par äldre fåglar omedelbart ifatt den osäkert flygande ungfågeln och puffade den underifrån.

Fylogenetiskt står tornseglaren (i ordningen seglarfåglar, Apodiformes) och hussvalan (i ordningen tättingar, Passeriformes) vitt skilda åt (Ericson 2008). Trots att båda arter är anpassade att själva luftburna föda sig på luftens innehåll av insekter och andra smådjur är de morfologiskt mycket olika. Detta gäller särskilt vingarnas utformning, som hos tornseglaren är karakteristiskt långsträckt och liebladsformad, vilket också ger tornseglarna och hussvalorna olika flygstilar. Olikheter här mellan arterna och hussvalans vita undersida, då den är synlig, har varit till hjälp vid artbestämningen. Förutom detta skiljer sig arterna i att hussvalan vid behov kan landa på och lyfta från marken, vilket inte tornseglaren kan.

HUR STUDIEN GJORDES

Baserat på de två observationerna ställde vi upp hypotesen att tornseglaren kan ge stöd i luften åt utflygande ungfåglar under deras första flygning. Vårt syfte här är att testa den hypotesen. Testverktyget är en flygande attrapp, Bionic Bird, i två varianter, det oförändrade originalet med dess breda vingar och en vars vingmembran klippts spetsiga (figur 2). Attrapperna drivs av en elmotor och ett laddningsbart batteri i kroppen. Flyghastighet och flygriktning regleras med en app i mobilen.

Testerna har gjorts på platsen för den första observationen (se inledning). Tornseglarkolonin där, ett 20-tal individer (figur 1a), häckar under taken på sommarhuset och ytterligare fyra hus i närheten. I närheten finns också en koloni hussvalor som häckar spridd på olika byggnader.

Vid lämpligt väder och närvaro av tornseglare ser man ganska snart reaktioner på attrappen med spetsiga vingar. Det blev snabbt två reaktioner, där den ena liknade ett förväntat stödjande beteende av en tornseglare (se resultat). Inte helt oväntat (se Tenow m. fl. 2008), visade sig den aktiva fågeln i det andra fallet vara en hussvala i stället för en tornseglare. Detta intressanta utfall av testet redovisas i detalj i resultatdelen.

Tornseglarens och hussvalans och beteende vid mötet med de flygande attrapperna dokumenterades med två videofilmer och två filmer tagna med en höghastighetskamera. De nämns här i den ordning de redovisas i resultatdelen: film 1 från tidig sommar 2016 (tornseglaren), film 2 från sensommaren 2016 (hussvalan), film 3 2020 (tornseglaren), alla tre med den spetsvingade attrappen, samt film 4 2015 med den bredvingade attrappen (tornseglaren). Dessutom synliggörs attrappens och hussvalors rörelser som banor, en metod (iskiografi) utvecklad av en av oss (LS, se Schiffler 2018). Ytterligare en film togs med snabbfilmskamera 4 augusti 2017 (av Andrzej Markiewicz, se diskussion).

Vid analysen av tornseglarens och hussvalans epimeletiska (vårdgivande) beteenden har här använts en klassificering som utvecklats för valdjur, t. ex. delfiner (jfr Tenow m. fl. 2008). Anledningen är att tornseglare och delfiner båda lever i icke bärande element, luft och vatten, och kan de inte hålla sig uppe (flyga eller simma) riskerar de att dö. Två huvudkategorier har urskilts och här anpassats till tornseglarens och hussvalans beteenden: ”succorant” (undsättande, stödjande), där vuxna riktar våden mot vuxna (i den mening att de förskaffar sin egen mat), samt ”nurturant” (uppfostran, ledande), där vuxna individer riktar vården mot unga individer som inte klarar sig utan matning. ”Succorant” har i sin tur delats upp i tre faser där den tredje fasen inkluderar om den utflugna individen ges stöd underifrån vid risk för kraschlandning.

RESULTAT

Resultaten visas här med stillbilder från de fyra filmerna, understödda av filmsekvenser ur filmerna. Tornseglarens och hussvalans möten med den spetsvingade attrappen redovisas i tidsordning. Figur 3 visar hur tornseglare cirklar omkring attrappen (figur 3a) och hur en av seglarna närmar sig attrappen bakifrån (figur 3b).

Hussvalans reaktion visas i tre steg med figur 4–6, där den följande är en förstorning av den föregående. Detta ger ett förlopp med allt snävare fokus och i allt större detalj (men minskad skärpa). Som ett första steg visar figur 4 med banor hur den spetsvingade attrappen och hussvalor flög under 22 sekunder av film 2. Under de 22 sekunderna flyger attrappen i två slingor, en övre tidigt under sekvensen och en undre i slutet av sekvensen. Steg 2 ger i figur 5 en förstoring av förloppet i den undre slingan, som visar hur en hussvala figurflyger ifatt (figur 5a), passerar under (figur 5b) och skils från attrappen när denna stiger brant uppåt och bakåt. I figur 5d sammanfattas panelerna i figur 5a–c. Steg 3 (figur 6) visar sedan i åtta stillbilder från videon i detalj hur hussvalan i figur 5b nalkas attrappen bakifrån och underifrån (figur 6a–b) och därefter riktar sig uppåt och stiger tills den är rakt under attrappen (figur 6b–c) samtidigt som den tätt under synkroniserar sina vingslag med attrappens, dock utan kroppskontakt (figur 6d–e). Därefter flyger den upp framför och i samma höjd som attrappen

(figur 6f–h) innan de skiljs som figur 5c visar. De åtta bilderna är suddiga men tolkbara (detaljer i tabell 2).

I figur 6 ses attrappen och hussvalan i stillbilder från sidan. Med film 3 dokumenterades mötet mellan attrappen och tornseglaren i stället i stillbilder bakifrån (figur 7). Den tolv sekunder långa filmen visar först hur en tornseglare kommer ner från skyn under sekund 5 från filmens början. De sex bilderna skildrar sedan förloppet inom sekund 6. Eftersom tornseglarens inflygning mot attrappen ses bakifrån (figur 7a–c) går det inte att avgöra om den verkligen flyger in under attrappen. I figur 7d tycks den vara beredd att passera under men ligger snett mot attrappen med högra vingarna korsade. Därefter skiljs paret (figur 7e–f). Det man säga är att tornseglaren påbörjade ett stödliknande beteende.

Stillbilder från film 4 (attrappen med breda vingar) används här för jämförelse med film 3 (spetsvingade attrappen). Stillbilderna i figur 8a–c från film 4, visar hur tre tornseglare, en efter en, dyker mot attrappen. Inom sju sekunder från frisläppandet av attrappen är det hela över. Den första kommer inom en sekund, den andra under sekund 5, och den tredje under sekund 7. Liknande dykningar mot attrappen skedde även när denna kommit upp i skyn som den fullständiga videon visar (supplement 5).

Film 1 togs 25 juni 2016. Attrappen var helt svart och attraherade tornseglare, medan hussvalorna inte syntes till. Film 2 spelades in 22 juli samma sommar. Vid hanteringen under mellantiden hade attrappens kroppsidor och mage blivit vita av slitage. Nu var situationen den omvända. Attrappen drog till sig hussvalor men inte tornseglare.

DISKUSSION

Vid mötet med attrappen med spetsiga vingar i film 3 visar tornseglaren ansatser till ett stödliknade beteende medan beteendet mot den bredvingade attrappen var klart avvisande och fientligt. Det finns skäl till detta fientliga beteende. Troligen uppfattas attrappen med sina breda vingar och mörka färg som en kråkfågel. Kråkfåglar är opportunister som gärna har småfågelungar och ägg på matsedeln, liksom fåglar som skadade har hamnat på marken. Det gäller säkert också unga tornseglare som misslyckats med sin debutflygning.

Frågan om ett luftburet epimeletiskt (vårdgivande) beteende hos tornseglaren har varit kontroversiell. Närmande av äldre fåglar till utflygande, osäkra ungfåglar har tolkats som aggression, t. ex. den rusning efter och trängsel omkring en ungfågel av kolonins medlemmar som man ibland kan se. Aggressionens mekanism skulle vara att genom angrepp testa, sålla ut och stöta bort svaga individer, ibland så drastiskt att ungfågeln skulle stötas ner till marken (Goethe 1939), dock inte iakttaget av rapportören, men tolkat så som förklaring till att ungfåglar ibland hittats skadade på marken. Tolkningen är alltså den direkta motsatsen till det som observerats av Tenow m. fl. (2008).

Intressant i sammanhanget finner vi att den helt svarta attrappen lockade tornseglare men inte hussvalor och att den svartvita attrappen lockade hussvalor men inte tornseglare. Förutom det förväntade i detta visar det, jämte vingarnas form, betydelsen av kroppens helt svarta yta och av svartvita partier, för identifiering av den egna arten.

Hussvalans beteende vid kontakten med den spetsvingade attrappen skildras ovan i tre steg. Vid det tredje steget närmar sig hussvalan och flyger upp mot attrappen. Ämnade hussvalan stötta attrappen underifrån på samma sätt som observerat hos tornseglaren? Lind (1960) ger, med sina noggranna och viktiga observationer av hussvalans beteenden, ett möjligt svar. Han visar att arternas epimeletiska beteenden är väsensskilda från tornseglarens och att frånvaron av kroppskontakt har andra, artspecifika orsaker. Hussvalan är en tätting där flygga ungfåglars förmåga att flyga effektivt lärs gradvis. En ungfågel flyger alltid ut tillsammans med och tätt efter en av föräldrarna vid sin första flygtur. Föräldern leder sedan flygturen som ibland för tillbaka till boet, där även övernattning kan ske. En utflugen hussvaleunge kan efter en kort flygtur slå sig ner en bit från boet och där bli matad av föräldrarna (figur 1 i Tenow m. fl. 2009).

I vår test var ”ungfågeln”, attrappen, redan på vingarna ensam. Hussvalan måste därför hinna ifatt den – och det snabbaste och mest effektiva sättet var att bakifrån och under med synkroniserade vingslag flyga upp framför attrappen (figur 6), för att därefter leda den på det sätt som Lind (1960) beskrivit. Viktigt här är att Lind (1960), i sin beskrivning inte nämner att äldre fåglar vid behov skulle passera under ungfågeln och stötta den underifrån. Anledningen är att ett sådant behov inte finns: en ungfågel som oskadd hamnat på marken kan sannolikt flyga upp igen.

En ung tornseglare har vid flygdebuten ingen läroperiod under sina föräldrar som mjukstart utan måste, för att inte kraschlanda, själv snabbt lära sig att flyga

effektivt och därefter söka sin föda själv. Av nödvändighet har därför hos tornseglaren utvecklats ett epimeletiskt beteende som innebär ett uppstödjande av en ungfågel i nöd. Det beteendet faller inom kategorin ”nurturant” eller ”succorant”, beroende på om ungfågeln betraktas som för tidigt utflugen eller som en ung adult, en fråga som här lämnas därhän. Enligt vad vi funnit här bör hussvalans epimeletiska beteende falla inom kategorien ”nurturant”. Beträffande ett ”nurturant” beteende hos tornseglaren, se Tenow m. fl. (2009).

Innan en räddningsaktion är möjlig måste en ungfågel i behov av hjälp kännas igen av de äldre. Föräldrar till mera markbundna arter känner igen sina egna på läten, dräkter och beteende och matas efter de lämnat boet. De snabbflygande tornseglarna känner sannolikt inte igen utflugna ungfåglar individuellt utan bara som art, antagligen på vingarnas form och flygsättet. En utflugen tätting i nöd kan skyddas av sina föräldrar där den sitter på sin gren. Tornseglarna har, som nämns i inledningen, (sannolikt) utvecklat ett mobilt, luftburet stödbeteende. En bakgrund till tornseglarens och hussvalans liknande beteenden kan sökas i deras historia.

Före människans besittningstagande av landskapet begränsades hussvalans och tornseglarens populationer sannolikt av tillgången på lämpliga boplatser. Hussvalan häckade på klippsidor i bergiga områden och längs vattendrag, även i grottor (Lind 1960). Tornseglaren förekom glest i urskogsområden där den häckade i gamla hackspettsbon. Med människans landtagande och tätnande bebyggelse skapades lämpliga boplatser i allt större mängd i håligheter i människans bostäder och uthus. De oskygga och sällskapliga fåglarna ökade då i antal och bildade dagens kolonier. I denna nya situation kunde inte föräldrar identifiera sina egna, utflygande ungar (se nedan).

Det är visat att tornseglare som fått en vilsekommen unge från ett annat bo, föder upp den som sin egen (Hahn & Yosef 2020). Man kan då anta att när ungfåglar flyger ut i kolonin kan föräldrar inte se eller känna igen om en viss ungfågel är deras eller inte. Däremot känner hussvalan sina egna utflugna ungfåglar, som Lind (1960) detaljerat beskriver.

För båda arter är ungfåglarnas debutflygning en händelse som engagerar kolonins medlemmar. När en hussvaleunge är redo förenar sig medlemmar i kolonin med föräldrarna, för att med läten locka ungfågeln att flyga ut. När den gör det, leder en av föräldrarna ungfågeln, som följer tätt efter på en rundtur som ibland leder tillbaka till boet (Lind 1960).

Samma kollektiva uppmaning till utflygning har iakttagits hos tornseglaren (Tenow m. fl. 2008). En utrusning omkring och efter den utflygande ungfågeln av kolonimedlemmar kan iakttas och tolkas som en sorts eskort. Det har också rapporterats att en tornseglare kommer ner från skyn och som en välkomsthälsning eskorterar den utflugna fågeln en kort stund innan den återvänder upp till skyn (Tenow m. fl. 2008 och referenser däri). Det vård- eller hjälpliknande beteende som hussvalor och tornseglare riktar mot attrappen med spetsiga vingar antyder att det hos båda arter finns ett hjälpande beteende oavsett om föremålet för beteendet är den egna avkomman eller inte.

SAMMANFATTNING

Vi har här visat på fyra beteenden hos hussvalan och tornseglaren som tidigare inte har uppmärksammats:

(1) Tornseglaren och hussvalan är känsliga för vingarnas form och kroppens färgteckning.

(2) Attrappen med spetsiga vingar bemöttes ”vänligt” av tornseglaren, den med breda vingar fientligt. Det senare emedan attrappen sannolikt uppfattas som en för ungfåglar farlig kråkfågel.

(3) Tornseglarnas och hussvalans beteenden mot attrappen med spetsiga vingar indikerar att föräldrar sannolikt inte känner igen sina egna utflygande ungfåglar.

(4) Tornseglarens och hussvalans luftburna epimeletiska beteende är väsensskilda: hos hussvalan ett uppfostrande/ ledande (”nurturant”) beteende efter artens speciella behov. Detta ger ett starkt, indirekt stöd för att också tornseglaren utvecklat ett undsättande/stöttande, helt och hållet luftburet, beteende efter dess speciella levnadssätt och behov av att rädda utflygande ungfåglar i nöd (indikerat i figur 7).

En direkt kroppskontakt har dock inte bevisats. Den fråga som ställs i titeln på artikeln Tenow m. fl. (2008) – ”do adults support young in flight?” – kan varken besvaras jakande eller nekande.