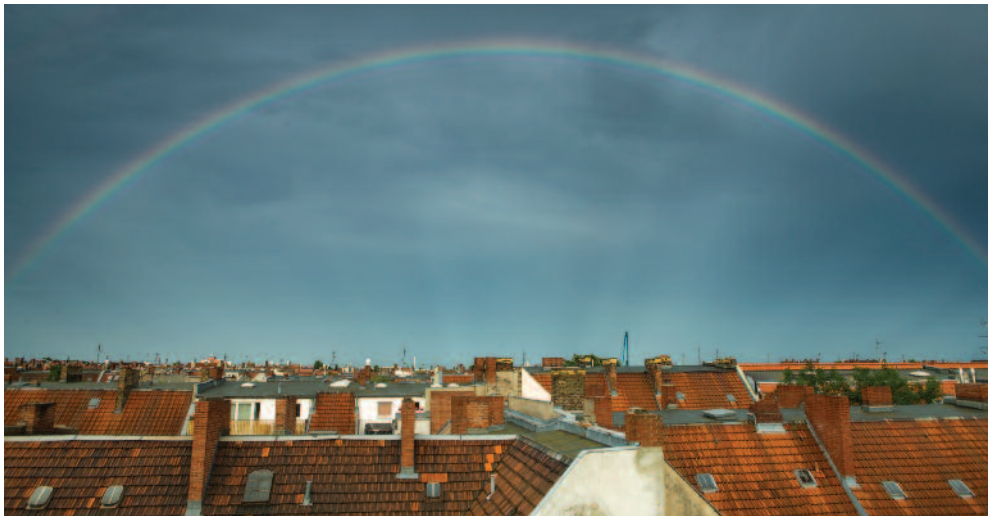
Behavioural thermoregulation in the Common Swift during flight

Christian Neumann

Abstract For the Common Swift *Apus apus*, which spends most of its life on the wing, thermoregulation during flight should be particularly important. For the first time, evaporative and non-evaporative thermoregulatory behaviour, chiefly trailing the legs but also gaping, were observed in flight; these are described and illustrated. At ambient temperatures exceeding 30°C, almost all Swifts observed were trailing their legs below the body; gaping (opening the bill) was also observed but less frequently. Leg trailing increases drag and thus represents a trade-off between optimal flight performance and cooling.

Like no other bird family, swifts are adapted to life on the wing. In fact, the Common Swift *Apus apus* (hereafter the Swift) spends the majority of its life in the air. Hunting, drinking, bathing and even nocturnal roosting take place while flying (Weitnauer 1952; Bäckman & Alerstam 2001; Lentink *et al.* 2007; Henningsson *et al.* 2009). Young Swifts spend almost two years on the wing without a break before they start breeding for the first time, in their third year (Glutz von Blotzheim & Bauer 1994). It is no wonder that these fast-flying birds show a number of morphological, physiological and behavioural adaptations to their airborne mode of life. The torpedo-shaped body is perfectly streamlined, the forked tail is short, and the curved, scythe-like wings are characterised by a short but powerful 'arm' and a long 'hand', with very long primaries. The feet of Swifts are proportionately smaller than those of most other birds, while the legs are short with a feathered tibia and a partially feathered tarsus. All four toes are unfeathered, each equipped with a powerful talon. Inappropriate for walking, the toes are used for



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162. The observation point, in the Schöneberg district of central Berlin, August 2014.

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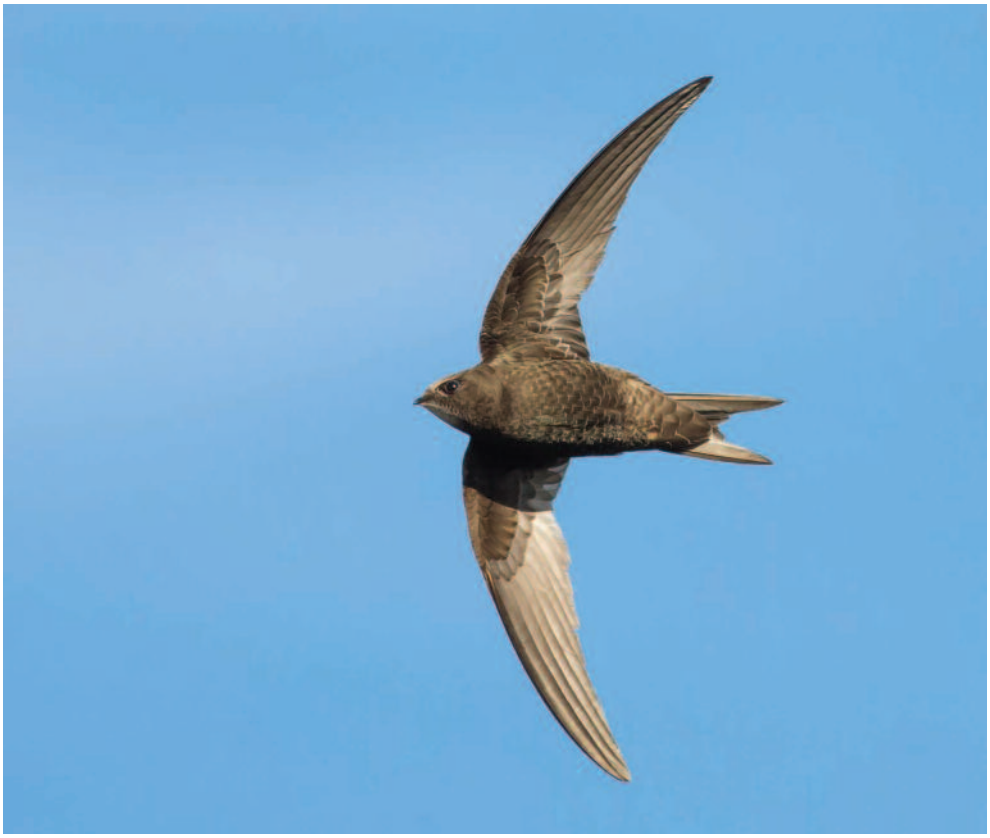

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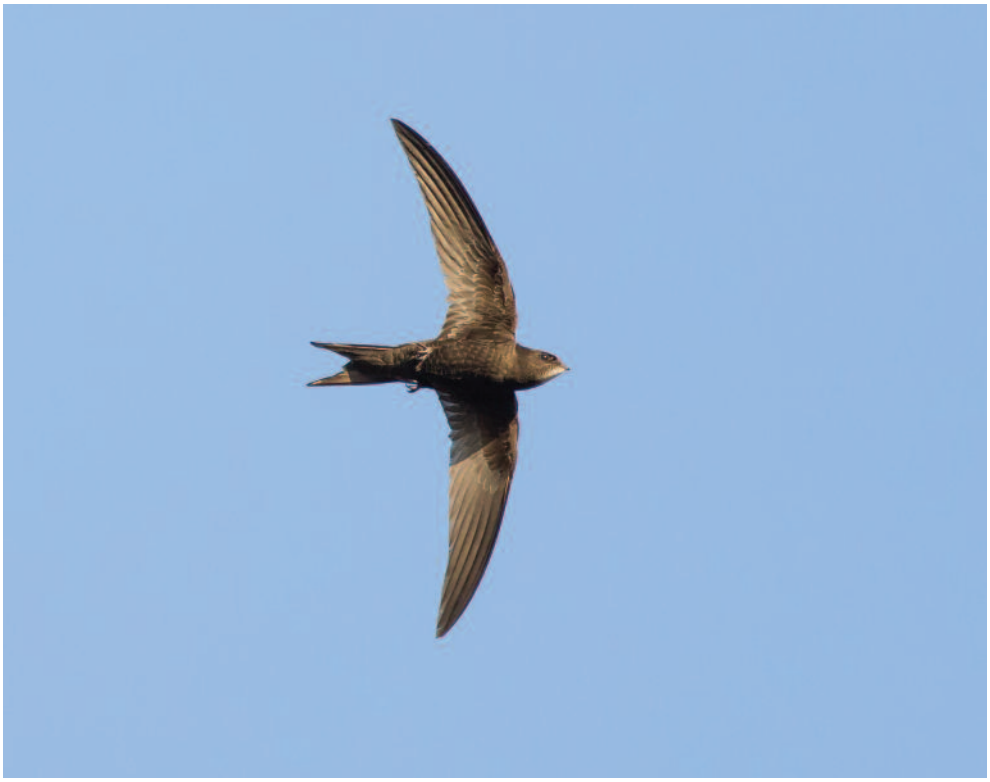
163. At moderate ambient temperatures, Common Swifts *Apus apus* fly with their legs retracted and hidden in the feathers of the vent to maintain an optimal aerodynamic body profile.

clinging to vertical surfaces at the nesting sites. During flight, the legs and toes are normally tucked up, hidden deep within the plumage of the vent, to achieve an optimal aerodynamic body shape. Indeed, the scientific name for the family 'Apodidae' means 'without feet' when translated from Ancient Greek (Glutz von Blotzheim & Bauer 1994; Chantler 1999).

Birds are endotherms (animals dependent on or capable of generating heat internally), which means that they tend to maintain their body temperature within certain limits. Other than at ambient temperatures, maintaining a constant body temperature makes a steady demand either on the biochemical processes of heat production or on the physical mechanisms of heat loss. To enable the body temperature to remain constant, a number of physiological and metabolic mechanisms and behaviours are necessary. For instance, the insulation properties of the feathers and lower metabolic rates are effective protection against low temperatures. Unlike most mammals, birds have no sweat glands, so evaporation as a way to counter overheating and to lose heat can occur only via the respiratory system, particularly by panting: breathing with an open bill (gaping) leads to evaporation and a subsequent fall in temperature in the mouth area. In many bird species, the effect of panting is supported by gular fluttering (Bartholomew *et al.* 1968; Dawson 1982; St-Laurent & Larochelle 1994). Another mechanism of heat loss is dissipation via unfeathered parts of the body – particularly the legs and the head – which are known to serve as efficient heat 'radiators' (Kahl 1963; Steen & Steen 1965; Ward *et al.* 2008). Leg trailing has been described for several passerine and non-passerine bird species – including pigeons (Columbidae), bee-eaters (Meropidae) and starlings (Sturnidae) – as a thermoregulative behaviour during flight (Frost & Siegfried 1975; Baudinette *et al.* 1976; Torre-Bueno 1976; Bryant 1983; Martineau & Larochelle 1988;



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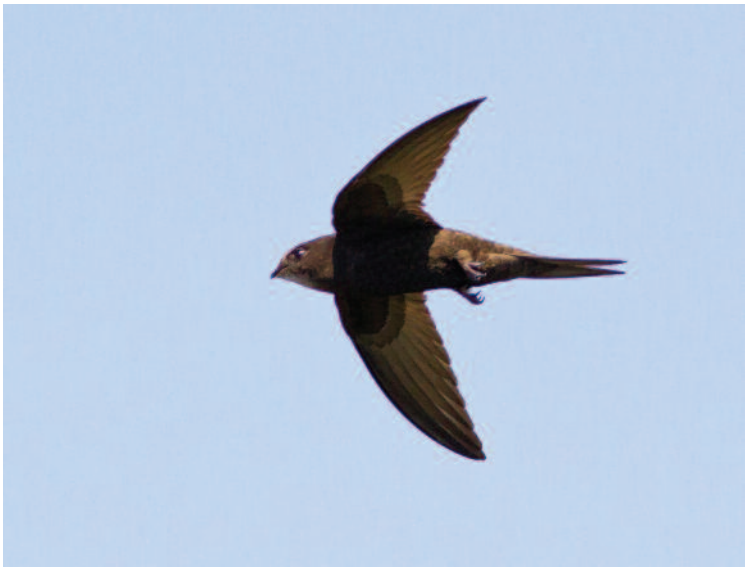
164. When ambient temperatures exceed 30°C, Common Swifts *Apus apus* may be observed flying with the legs trailing down from the body, and the toes well spread.

Ward *et al.* 1999). Such leg-trailing behaviour is thought to be especially important for birds inhabiting open areas, where there are limited opportunities to seek shade from the sun's heat (Bryant 1983). For Swifts, living permanently on the wing and thus particularly exposed to solar radiation, behavioural thermoregulation during flight would be expected to be extremely important. Both leg trailing and panting have been studied in the Common Swift and, apart from a brief note by the author (Neumann 2015), are described in detail and illustrated here for the first time.

Study area and methods

Leg-trailing behaviour in the Common Swift was first noticed by the author by chance during a hot summer day in Berlin, Germany, in 2012. In subsequent years (2013–15), more systematic observations of this phenomenon were carried out. The study was undertaken in the Schöneberg district of central Berlin. Observations were made from the roof of an apartment building (22 m above ground), which provided all-round visibility of the adjacent skies (plate 162). Swifts breed commonly in central Berlin, and the distance from the vantage point to the nearest breeding colony is about 150 m. Up to 60 Swifts at any one time were counted during each observation session, using the air space around the observation point for hunting and social display flights. Observations were carried out in May, June and July. Since Swifts tend to fly at higher elevations in the middle of the day, most observations were made in the morning and evening (predominantly about two hours after sunrise and before sunset) but were occasionally carried out during the middle of the day as well. Owing to their speed of flight, close observations of Swifts with the human eye are almost impossible, so all the Swifts passing within close range of the observation point (approximately within 50 m) were counted and photographed using a full-frame digital SLR camera and a 400 mm f/5.6 telephoto lens. To achieve sufficiently sharp images, shutter speeds of 1/2000 s or faster were used. Post-processing of the digital images included cropping and tonality adjust-

ments to reveal details. Only images showing the bird's ventral side or body profile were considered. Image analyses included the registration of leg trailing and gaping. Air temperatures during the observation periods were measured to an accuracy of 1°C using a standard thermometer.



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165. The legs can be trailed to a level so that the whole tarsus is exposed.

Results

The results of the field observations are summarised in table 1. Observations were made on 29 days with a total of 31 hours of observation (mean observation time/day: 1.06 hours). During this time, separate observations of 1,511 flying Swifts were made and suitable photographs obtained. The majority of observations were made in July (16 days) followed by June (eight days) and May (five days).

On three observation days (27th July 2013, 17th and 22nd July 2015) the ambient temperature during the observation period was 30°C or higher. This corresponded exactly with the days when leg trailing was noted. On 27th July 2013, leg trailing was observed on 95% (93/98) of all photographed flying Swifts; on 17th July 2015, leg trailing was performed by 96% (68/71); and on 22nd July 2015 by 91% (59/65) of all photographed individuals where either the belly or the body profile was visible. At lower ambient temperatures, Swifts always flew with their legs retracted and the feet hidden in the body feathers (plate 163). At temperatures above 30°C, most Swifts were observed with their feet extending down below the body, mostly with the toes well spread (plate 164). On many occasions, the legs were extended to the extent that the whole tarsus was also exposed (plate 165). On two of the days when leg trailing was observed, gaping was also recorded, albeit to a much lesser extent: on 27th July 2013 and 17th July 2015, some birds (4% and 12%, respectively) flew with their bill slightly open, a behaviour otherwise not observed (plate 166). At moderate ambient temperatures, all Swifts tend to fly with the bill closed; it is opened only for foraging and vocalisations (plate 167).

Discussion

Unfeathered parts of hind limbs serve as heat radiators

The important role of unfeathered parts of birds' legs in non-evaporative thermoregulation (i.e. convection and radiation) was described by Steen & Steen (1965) and Baudinette *et al.* (1976). The toes of the Common Swift are unfeathered, while the tarsus is thinly feathered at the front and unfeathered at the rear. At ambient temperatures exceeding 30°C, the toes and the tarsi are typically trailed and the toes are spread to increase the surface area exposed to the wind. This confers a sensitive mechanism to regulate heat loss through behavioural control of the heat exchange area. These observations were confirmed by wind tunnel experiments using Feral Pigeons *Columba livia* (Biesel & Nachtigall 1987). The researchers concluded that birds' legs fulfil all the requirements for an effective, well-controlled heat-loss system.

The trade-off between optimal flight performance and the cooling effect

Leg trailing increases drag during flight. This

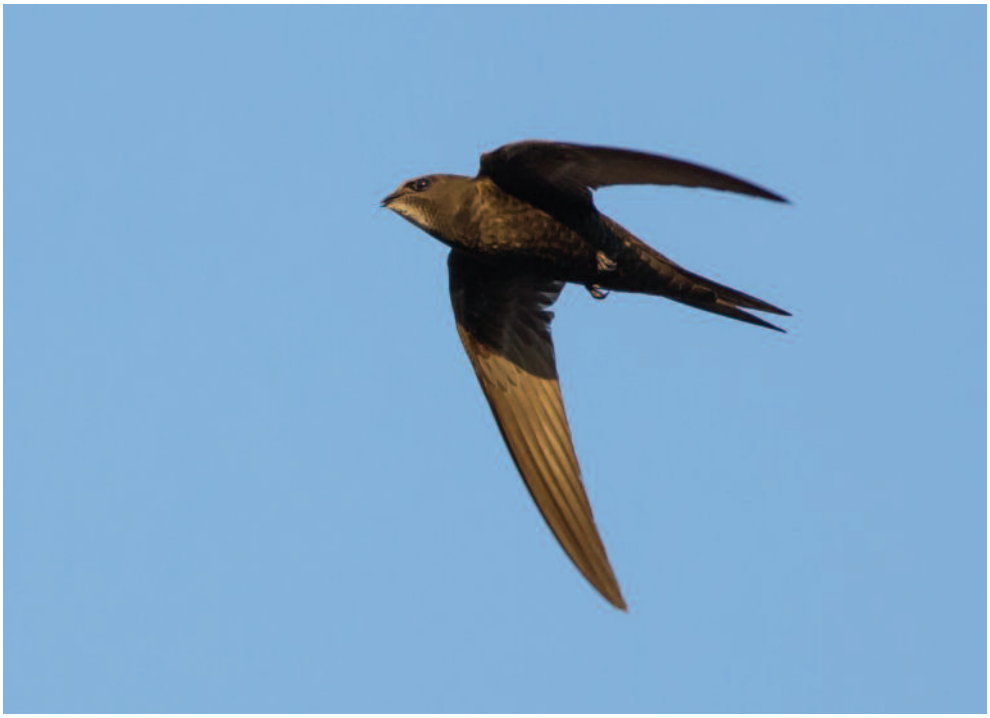
Table 1. Observations of behavioural thermoregulation (leg trailing and gaping/bill opening) in the Common Swift *Apus apus* in Berlin, Germany, 2013–15.

date	observation time (UTC+2)	duration (minutes)	max. temp (°C)	no. birds photographed	leg trailing	gaping
17.05.2013	19.21–20.37	76	24	48	0	0
19.06.2013	05.18–08.13	175	19	95	0	0
21.06.2013	20.56–21.19	23	22	17	0	0
22.06.2013	20.40–21.17	37	23	35	0	0
02.07.2013	20.13–21.03	50	20	35	0	0
04.07.2013	20.21–21.23	62	20	52	0	0
09.07.2013	06.12–08.21	129	18	92	0	0
17.07.2013	07.49–08.34	45	19	39	0	0
26.07.2013	07.25–07.50	25	20	19	0	0
27.07.2013	10.34–12.21	107	33	98	93	4
19.05.2014	18.27–20.51	144	20	112	0	0
21.05.2014	19.56–20.18	22	26	21	0	0
22.05.2014	07.30–08.18	48	19	35	0	0
26.05.2014	19.08–20.01	53	24	44	0	0
04.06.2014	19.39–20.54	75	22	60	0	0
26.06.2014	07.49–08.17	28	16	17	0	0
02.07.2014	07.38–08.31	53	16	29	0	0
12.06.2015	17.38–20.03	145	26	98	0	0
24.06.2015	20.36–21.05	29	15	19	0	0
25.06.2015	15.44–17.00	76	23	46	0	0
01.07.2015	20.55–21.22	27	24	20	0	0
02.07.2015	20.35–21.12	37	27	29	0	0
07.07.2015	07.04–07.47	43	27	55	0	0
16.07.2015	19.38–20.38	60	24	49	0	0
17.07.2015	19.22–20.04	42	30	71	68	9
18.07.2015	06.07–07.17	70	18	62	0	0
21.07.2015	19.33–20.43	70	22	78	0	0
22.07.2015	13.26–14.39	73	30	65	59	0
23.07.2015	07.39–08.56	77	23	71	0	0

is particularly significant for Swifts, which are extremely fast-flying and habitually aerial birds, able to glide at an average speed of 11 m/s (Videler *et al.* 2004) and to fly twice as fast (20.9 m/s during social display flights and up to 31.1 m/s for shorter periods; Oehme 1968; Bruderer & Weitnauer 1972; Henningsson *et al.* 2010). Swifts have evolved a perfectly streamlined body profile with low drag to match the aerodynamic needs for high-speed flying (Lentink *et al.* 2007). Leg trailing should therefore represent a trade-off between optimal flight performance and effective heat dissipation. The fact that Swifts accept the disadvantages in flight speed and manoeuvrability emphasises the need for thermoregulation during flight and the importance of legs and feet for heat dissipation.

Leg trailing vs panting

Why was panting behaviour observed much less frequently than leg trailing in this study? Two different explanations for this are suggested. First, high-speed flight with the bill wide open would be disadvantageous because of the high risk of unwanted detritus entering the mouth. Second, evaporative thermoregulation by panting should be avoided by birds living in hot and arid environments since there is an increased risk of water loss and dehydration (Torre-Bueno 1976; Dawson 1982; Biesel & Nachtigall 1987; Carmi *et al.* 1992). The breeding range of the Common Swift includes many areas with hot summer temperatures, for example southern Europe, parts of North Africa and the Middle East (*BWP*). Moreover, Swifts spend two-thirds of their life in the hot regions of equatorial and subequatorial Africa and therefore it seems likely that leg trailing is the preferred method of thermoregulation compared with panting. It is assumed that Swifts first developed this



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166. In addition to leg trailing, thermoregulation can be enhanced by gaping, with the bill slightly open.

behaviour in the warmer regions of their range and then used it in more temperate breeding areas when their range expanded northwards after the last glaciation.

Potential conflict with ringing

Legs are important thermoregulatory organs not only for Swifts but also for many other species, both non-passerines and passerines. For species that habitually use the legs for thermoregulation, the use of multiple colour rings on the tarsi may hamper convective heat loss of the covered skin surface. It is likely to be a problem mainly for species such as the Swift, which is airborne with the legs retracted for such a high proportion of daylight hours. Using a simple experimental design to explore this potential problem would be worthwhile.

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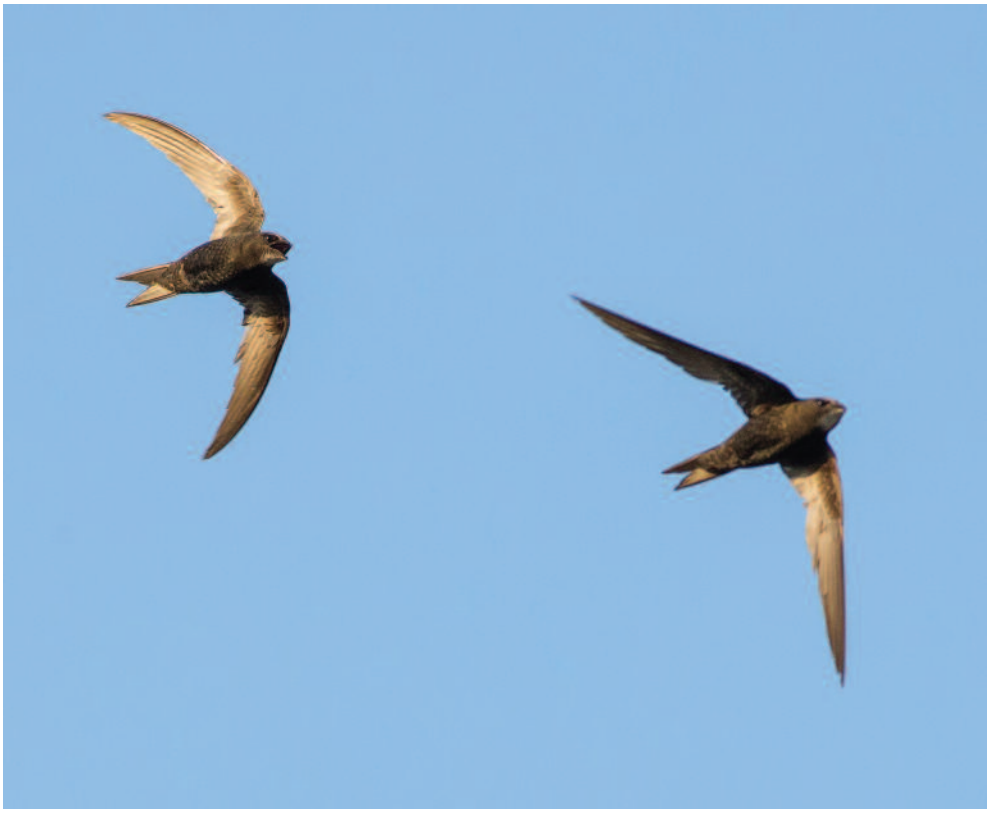

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167. At moderate ambient temperatures, swifts open their bill only for foraging or vocalisations (as here).

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