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Slight sexual dimorphism in tail-fork depth of Common Swifts *Apus apus*

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ABSTRACT

For two new data sets from the Netherlands, we show that male Common Swifts have deeper tail forks than females. Although this hints at sexual selection, with a degree of masculine extravagance at work, the male dimensions are closer to the design rules for an aerodynamically optimal swift than are those of females.

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The swifts Apodidae stand out among birds for their uniquely aerial lifestyle, with foraging, feeding, mating and sleeping all carried out on the wing (Chantler 1999, Foster 2021). During the breeding season though, birds have to come back to nests which can hold eggs and young. The majority of species breed in holes in hard substrates or in nests made of saliva and feathers, usually at locations which are only accessible through flight. The idea that non-breeding swifts may spend almost all of their time, by day and by night, on the wing (Lack 1956, Lockley 1969) has now been documented for several species (Liechti *et al* 2013, Hedenström *et al* 2016, 2019). The aerodynamic sophistication of the typical swifts, of the tribe Apodini (Lentink *et al* 2007, Hedrick *et al* 2018), is expressed in their slender curved wings and their short and shallowly forked tails (Thomas 1997).

Swifts are considered to be sexually monomorphic, although the general texts on swifts are not very explicit on this point (e.g. Chantler 1999). Nevertheless, sexual differences in the length of wing and tail have been documented for Plain Swifts *Apus unicolor*, with the males being the slightly larger sex (Garcia-Del-Rey *et al* 2008). In Pallid Swifts *Apus pallidus*, Boano *et al* (2015) found no sexual dimorphism in the lengths of the eighth primary and the rectrices, but they did with respect to wing length, with males being a little larger than females. Although

a sample of adult Common Swifts *Apus apus* from Switzerland showed males to be 1–2% larger than females with respect to the lengths of wing, tail and carina (the keel of the breastbone) (Glutz von Blotzheim & Bauer 1980, Cramp 1985), this extent of sexual size dimorphism was ignored in subsequent in-depth studies of their migration (e.g. Åkesson *et al* 2012, 2020). Yet, sexual dimorphism, even if slight, is interesting, as it may inform us about the relative degrees of natural and sexual selection (Zhu *et al* 2020).

To assess these selection pressures, we have to understand the evolutionary development of tails for different functions (Thomas 1997). Tails help to maintain aerodynamic stability. During flight at low speed they add lift to that provided by the wings, but during fast flight they produce lift only during acceleration and turning. This means that during fast flight the tail is used as a rudder to enhance manoeuvrability, and this function is optimised if the outer feathers are about twice the length of the central feathers (Thomas & Balmford 1995, Thomas 1997). In a sample of 101 Common Swifts captured between May and July in the Netherlands, this ratio is about 1.7 (HvdW *et al* pers obs). With their slender wings and their forked tails, Common Swifts therefore count as particularly aerodynamic birds (Thomas 1997). In this note we present an analysis of two new data sets on body size for internally or molecularly sexed

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Common Swifts from the Netherlands. Unlike other body-size measurements, the depth of the tail fork showed a fair degree of sexual dimorphism. Does this hint at sexual selection after all (Balmford *et al* 1994)?

Material and Methods

From May to July in 2011 and 2012, a field study was carried out in the village of Pingjum, Friesland, the Netherlands (53°07'01"N 05°26'22"E). Enclosing an open lawn, three sets of two mist-nets placed one above the other made it possible to catch, at heights of about 6–7 m, Common Swifts flying around an adjacent high-rise building. The birds were attracted by a sound system which played their contact calls continuously. All catching was carried out by HvdW, throughout entire days, but depending on time available and weather (see Jukema *et al* 2015).

Swifts in their second calendar year were distinguished from adults by their abraded and lighter-coloured primary feathers. We measured the stretched wing with a stopped rule, and the depth of the tail fork (the distance between the tips of the outer and inner tail feathers) with a rule, both to the nearest whole millimetre. A droplet of blood was collected from the brachial vein after a small puncture with a sterilised needle. Blood was drawn with a heparinised microcapillary tube and the puncture closed using a small piece of cotton wool. The blood was stored in 96% alcohol at -20°C before DNA extraction. DNA was extracted in the laboratory using the salt extraction method of Richardson *et al* (2001). Birds were sexed by PCR amplification of a part of the CHD gene that is located on the sex chromosomes following Van der Velde *et al* (2017). The annealing temperature of the PCR reaction was adjusted to 58°C. PCR products were separated on 2% agarose gels with males showing one band and females two bands.

A second data set comes from the measurements of all Common Swifts available as skins in the collection of National Natural History Museum Naturalis, Leiden. These birds were all adult and had died from a variety of causes in summer months between 1856 and 2012. All measurements were taken by JJ.

Preliminary Shapiro–Wilk tests indicated that both wing and tail-fork measurements of immature Common Swifts captured in Pingjum followed a non-normal distribution (wing $W = 0.978$, $P = 0.0072$; tail fork $W = 0.956$, $P = 0.0001$). Thus, we evaluated sexual dimorphism in tail-fork and wing lengths with unpaired two-sample Wilcoxon tests, in both cases for immatures and adults separately.

Results and Discussion

The slight sexual dimorphism, with males being 1–2% larger than females, documented by Glutz von Blotzheim & Bauer (1980), was confirmed in the wing length of the Dutch sample of immatures (Table 1). In contrast, tail forks were 3–7% deeper in males than in females in all three samples (Table 1, Figure 1). For the two new samples these differences were statistically significant in both the immatures captured alive in summer (Wilcoxon rank sum test, $W = 3946$, $P < 0.001$) and the adults stored as skins in Naturalis (Wilcoxon rank sum test, $W = 3664$, $P = 0.007$). Similarly, wings were longer in immature males than in immature females (Wilcoxon rank sum test, $W = 5039$, $P < 0.001$).

The deeply forked tail of male Barn Swallows *Hirundo rustica* has been argued to represent a strongly sexually selected trait (Møller 1994), and indeed their tail feathers are longer than would be expected for optimal rudder function during fast flight (Thomas & Balmford 1995, Thomas 1997). In the Common Swifts studied here, the deeper forks of males would come closer to this ideal than the forks of females, so this would argue for the tail forks of males to be ‘naturally’ rather than ‘sexually’ selected. But why would females have shallower tail forks than males, and deviate more from a predicted optimal body shape?

Elucidation of these selection pressures on tail morphology would obviously be complex and difficult. It calls for more comparative work, in different species and across different populations exposed to different ecological regimes, and experimental studies on aerodynamic performance, in wind tunnels as well as in the wild.

Table 1. Sexual dimorphism in three external body dimensions of Common Swifts sampled in Switzerland and the Netherlands: wing length, length of the outer tail feather and tail-fork depth. Data are mean \pm standard deviation (mm) and, for each sample, the male:female ratios of the mean values. Where n has two values, the first value is for wing and tail and the second for fork depth.

| Sex | n | Wing length | Tail length | Fork depth |
|--|----------|-----------------|----------------|----------------|
| <i>Adults freshly dead in Switzerland, measured by E. Sutter (Glutz van Blotzheim & Bauer 1980)</i> | | | | |
| Male | 181, 179 | 174.6 \pm 3.7 | 76.6 \pm 2.6 | 30.8 \pm 1.9 |
| Female | 159 | 172.9 \pm 3.4 | 75.4 \pm 2.4 | 29.2 \pm 2.0 |
| Male:female | | 1.009 | 1.016 | 1.055 |
| <i>All available Dutch skins of adults in National Natural History Museum Naturalis, Leiden, collected between 1856 and 2012, measured by JJ</i> | | | | |
| Male | 86 | – | – | 31.3 \pm 2.5 |
| Female | 68 | – | – | 30.3 \pm 2.5 |
| Male:female | | – | – | 1.034 |
| <i>Molecularly sexed immatures at Pingjum in May–July 2011, captured by HvdW and measured by JJ</i> | | | | |
| Male | 92, 77 | 173.8 \pm 2.9 | – | 30.2 \pm 2.1 |
| Female | 92, 75 | 172.4 \pm 3.2 | – | 28.8 \pm 2.2 |
| Male:female | | 1.008 | – | 1.049 |

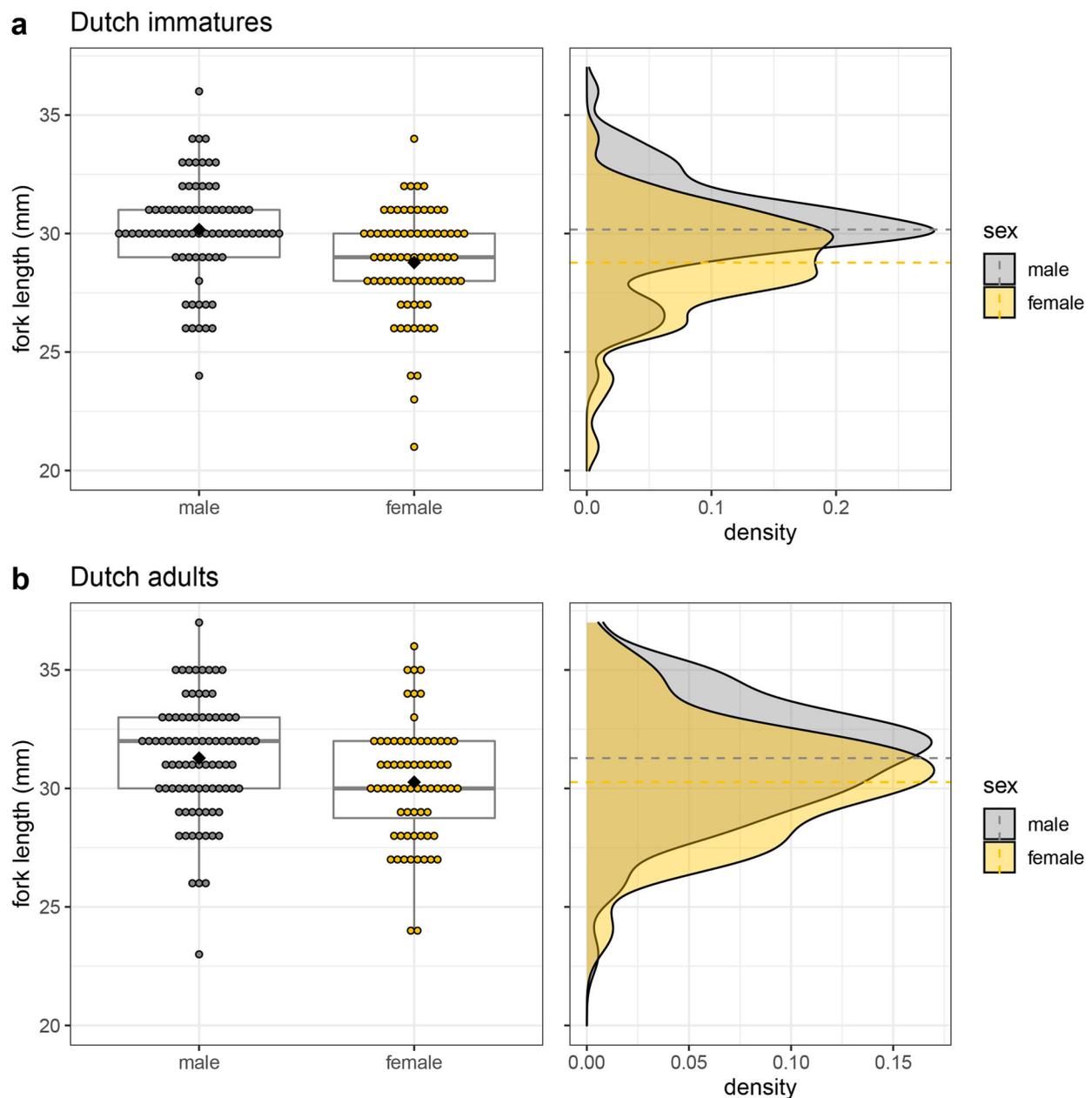


Figure 1. Sexual dimorphism in the tail forks of Common Swift from the Netherlands: (a) immatures captured in May–July 2011 in the north of the Netherlands; (b) skins from across the Netherlands in the collection of Naturalis, Leiden. Box-and-whisker plots give medians (horizontal line), means (diamond), interquartile ranges (box), ranges (bars). Density plots also indicate the mean value for each sex.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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