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Sexual size dimorphism and moult in the Plain Swift *Apus unicolor*

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The biometrics and moult of swifts are poorly known, yet represent important aspects of their breeding biology. In this study we investigated moult and used molecular sexing to characterise sexual size dimorphisms in the Plain Swift *Apus unicolor*. In contrast to previous work based on skin specimens, males were significantly larger than females with respect to wing length (2.0 mm difference) and tail length. The sexes did not differ in body mass. We derived a discriminant function by binary logistic regression to separate the sexes using wing, bill and tail length; the function was accurate in assigning 70% of the birds to their correct sex. Moult data obtained from 30 birds suggested that almost 25% of individuals overlapped breeding with the start of moult (estimate: 16 August ± 20 days) and that the progress of primary-feather moult was slow and initiated from at least two moult centres. Further studies are needed to investigate moult in relation to migratory strategy in this swift species.

Many bird species show strong sexual size dimorphism, and in extreme cases one sex may be twice the weight of the other (*eg* in raptors, in which females are the larger sex: del Hoyo *et al* 1994; and bustards, in which males are larger: de Juana 1994). In most birds, the male is slightly larger than the female, and it is assumed that this reflects different selection pressures on the sexes related to differences in ecology (*eg* feeding habits), intra- and intersexual agonistic interaction, and mate selection (Lack 1968). Bennett & Owens (2002) confirmed that, across species, sexual size dimorphism is closely related to the social mating system and sex differences in the extent of parental care, but they also suggested that the direction of size dimorphism might be tied to the relative roles of sexual selection and niche division in promoting divergence between the sexes. The degree of sexual dimorphism may be an indicator of the strength of sexual selection (Badyaev & Hill 2003) so that studies of dimorphism do not only serve to provide a practical method for sexing birds measured in the field (*eg* Fox *et al* 1981, Hanners & Patton 1985), but might also offer a first assessment of the intensity of sexual selection within the species studied.

Several methods have been employed to sex species that are sexually monomorphic in plumage: (1) behaviour of breeding birds, which is only possible during the breeding season and not suitable for sexing outside the reproductive period (Fox *et al* 1981); (2) vent measurement, which is only useful for a short period after the female has laid her eggs (Newton 1989); (3) laparotomy, in contrast, can be used throughout the year, but is very intrusive and time consuming (Sutherland *et al* 2004); (4) DNA analysis; or (5) morphological criteria. Sexing birds by DNA analysis is by far the most widely applicable technique and only requires a small sample of blood or a feather (Kahn *et al* 1998, Baker *et al* 1999, Ristow & Wink 2004, Sutherland *et al* 2004). Alternatively, for many species, sexing has been achieved successfully by discriminant analysis using morphological external measurements (Anderson 1975, Green 1982, Butler & Gosler 2004).

The unique aerial lifestyle of swifts Apodidae has meant that, as a group, their biology is poorly known, particularly with respect to sexual dimorphism. The Plain Swift *Apus unicolor* is a Western Palearctic species restricted to the Atlantic Islands of Madeira and the Canaries (Bannerman 1963) (see Fig 1), where it occupies most of the islands of the two archipelagos. It is very similar to the Common Swift *Apus apus* except that it is about 20% smaller (Cramp 1985) and has a darkish throat (Lack 1973). The Plain Swift is a colonial breeder that nests in caves or fissures of cliffs (Chantler & Driessens 2000), under bridges (Garcia-del-Rey 2006) and in holes in the bricks of unfinished houses (pers obs), but it will also make use of artificial nestboxes

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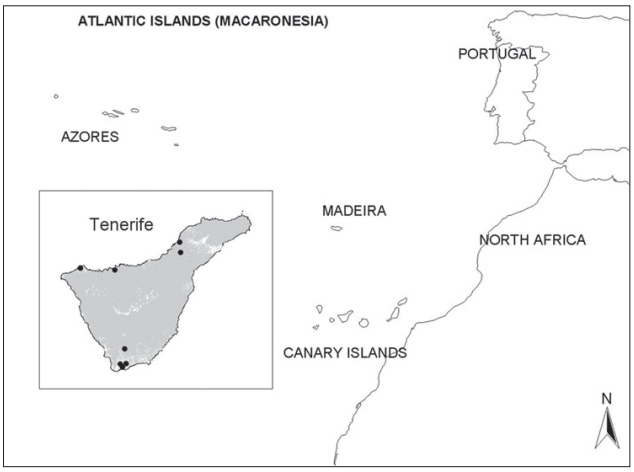

Figure 1. Distribution of colony locations (•) on the island of Tenerife where Plain Swifts were ringed during the course of this study (2002–06).

(this study). As in most swift species, it has a prolonged breeding season (early March to mid September in Gran Canaria), but reproduction seems to be adapted to the geographical location and oceanic aspect of these islands (Garcia-del-Rey 2006). Despite the unique endemic status of the Plain Swift, all external measurement data presented in the literature for this species has come from a very few skin specimens, and these data suggest that, as in most swifts, the sexes are similar; furthermore, no information on weights of live birds is yet available (Chantler & Driessens 2000, Cramp 1985). It is well known that, when skins dry, a slight shrinkage affects particular measurements (*eg* wing length: Svensson 1992), and this limits the value of comparisons between skin specimens and live birds in the field.

The ability to determine readily and accurately the sex of ringed Plain Swifts would enable sex-specific survival rates to be quantified, analysis of sex ratios within and between flocks to be undertaken, and other aspects of Plain Swift population dynamics to be quantified. In this paper we present biometric and moult data collected from live birds, measured using standardised methods (Redfern & Clark 2001), and investigate sexual size dimorphism of the Plain Swift using molecular techniques.

METHODS

Study site and biometrics

Over the course of this study (from 11 July 2002 to 20 September 2007), 208 adult Plain Swifts were ringed. All were caught using mist nets, measured and aged, at eight colony sites on Tenerife (see Fig 1). All biometric measurements reported here were taken by EGDR.

Wing length (maximum chord) was taken using a stopped rule (Redfern & Clark 2001) to 1 mm. Bill length (tip to skull) and bill depth (at distal edge of nostril) were measured to 0.1 mm using digital callipers. Tail length (interior and exterior) was measured using an unstopped rule to the nearest 1 mm (base of the uropygial gland for the exterior). To measure body mass, birds were weighed on a 50 g Pesola balance to 0.1 g and the time of weighing recorded. Moult was recorded using the method described by Ginn & Melville (1983) (after Newton 1966) in which each flight feather is given a score from 0 (old) to 5 (fully grown and new).

During the autumn of 2005, fifty nestboxes were set up at one of the colonies (Arona: 28°55'N 16°37'W) as part of a long-term study started by Sociedad Ornitologica Canaria. This enabled the monitoring of chicks in the nest. In an attempt to detect those features that best separate juvenile birds from adults, chicks near fledging were photographed with a digital camera during the 2006 breeding season.

Molecular sexing methods

Blood samples from 79 adult individuals were obtained by venipuncture of the brachial vein, as in Hawkins *et al* (2001, p162). Total DNA was isolated from 100 µl of blood using standard Proteinase K (Merck, Darmstadt) and phenol/chloroform procedures (Sambrook *et al* 1989). Sex identification was as described by Kahn *et al* (1998). Polymerase Chain Reaction (PCR) was performed with 30–60 ng of template DNA in a 25 µl reaction volume containing 8 pmol of the primer H1272 and 9 pmol of the primer L1237, 0.1 mM of 2'-deoxyguanosine 5'-triphosphate, 2'-deoxycytidine 5'-triphosphate, and 2'-deoxythymidine 5'-triphosphate, 0.045 mM 2'-deoxyadenosine 5'-triphosphate (dATP), 37 kBq [α'-^{33}P]-dATP (Amersham Biosciences), 0.6 units of Taq-Polymerase (Pharmacia Biotech, Freiburg) and 2.5 µl of 10x amplification buffer (50 mM KCl, 1.5 mM $MgCl_2$, 10 mM Tris-HCl, pH 8.5). Each reaction was overlaid with two drops of mineral oil. Thermo-cycling was performed with a Trio Thermo block TB1 (Biometra, Göttingen). After the initial 5 min denaturation at 94°C, the program consisted of 31 cycles of 30 s at 94 °C, 40 s at 56°C, 40 s at 72°C and 5 min at 72°C for the final elongation. DNA fragments were separated by vertical polyacrylamide gel electrophoresis for 2 h at 65 W using a Base Acer Sequencer (Stratagene). After drying, the denaturing gels were exposed for 24 h to X-ray film (BioMax MR Film, Kodak) and the bands analysed visually. The presence of two bands was scored as female and one band as male (Kahn *et al* 1998). Biometrics from individuals of known sex were then pooled and a logistic regression function was derived.

Data analysis

A Kolmogorov–Smirnoff test was used to check if the variables were normally distributed. A Student t-test was used as a first attempt to analyse biometric differences between the sexes. A Principal Component Analysis was carried out in CANOCO 4.5 to summarise biometric characteristics of the Plain Swift sample. The PC scores of each factor were used to compare the different groups. Finally, a binary logistic regression function was calculated. In accordance with assumptions of the model, all birds were measured only once (*ie* no recaptures were used in the analyses). Data for moult scores and the presence or absence of moult were used to obtained maximum-likelihood estimates for moult start date and standard deviation (SD) by fitting a type 2 model as described by Underhill & Zucchini (1988). The model was fitted to the data using a computer program written in 'R' by Walter Zucchini. All other statistical analyses were performed using SPSS 12.0 and results are presented as mean ± standard deviation (Zar 1996).

RESULTS

Mean biometrics for males and females confirmed by DNA analysis, as well as swifts of unknown sex, are shown in Table 1. Between the sexes, statistically-significant differences were found for wing length (t= -2.64, df= 77, P<0.05), tail length (interior, t_{77}= -2.44, P<0.05; exterior, t_{77}= -2.25, $P < 0.05$), but not for tail-fork length (t_{77}= -0.47, $P > 0.05$; see Table 1). However, both tail interior and tail exterior lengths were significantly correlated with fork length (Pearson r = -0.72, $P = 0.0001$, n = 109; Pearson r = 0.61, $P = 0.0001$, n = 109, respectively). No statistically-significant differences between the sexes were observed for other biometric measurements (bill length, t_{77}= -1.58, $P > 0.05$; bill depth, t_{77}= -0.26, $P > 0.05$ or mass, t_{77}= 0.79, $P > 0.05$). Of these measurements, only mass showed a weak correlation with bill length (Pearson r = -0.20, $P = 0.03$, n= 129). Hence, male wing length was on average 2.0 mm longer than that of females and males also showed longer tails, on average, than do females (1.0 mm tail interior and 1.0 mm tail exterior).

A Principal Component Analysis (PCA) was used to group the biometric variables (see Fig 2). A set of two factors explained 71% of the total variation (Table 2). The first factor (PC1) was related to wing and tail fork where males were significantly larger than females (one-way ANOVA, F = 4.26, $P < 0.05$). The second factor (PC2) was related to bill length, tail interior and mass, but was not significantly different between the sexes (PC2, F = 0.70, $P > 0.05$). The relationship between males and females in the ordination space is shown in Fig 3.

Sexing

A binary logistic regression function was calculated to predict sex from wing length, bill length, bill depth, tail (interior), tail (exterior), fork and mass (n = 79). Backwards deletion of the variables was used so that only those elements that were at least weakly significant ($P < 0.1$) were retained. This generated a significant binary logistic regression function (α_2 = 17.1, df = 3, Nagelkerke $R^2 = 0.26$, $P < 0.001$), which included only wing length, bill length and tail (interior) as parameters:

x = (–0.187 wing length) – (0.937 bill length) – (0.464 tail interior) + 58.992

This logistic function gives a negative value of x for males and a positive value for females, and was accurate in assigning 70% of the birds sexed by DNA analysis to their appropriate sex. All elements of this function were significant (Table 3), and from this adult birds with a wing length of 143–147.5 mm could be sexed as female with 100% confidence (see ranges in Table 1).

Table 1. A summary of the biometrics for Plain Swift in Tenerife during this study. Data are means ± standard deviation, range (in parentheses), and sample size.

	Wing (mm)	Bill length (mm)	Bill depth (mm)	Tail interior (mm)	Tail exterior (mm)	Fork (mm)	Mass (g)
All	152.3 ± 3.0	9.7 ± 0.8	2.2 ± 0.2	45.5 ± 2.8	73.3 ± 2.4	28.3 ± 2.7	22.5 ± 3.1
	(142.0–158.0)	(7.6–11.6)	(1.7–2.9)	(42.0–68.0)	(66.0–79.0)	(21.0–33.0)	(18.4–30.0)
	n = 143	n = 129	n = 129	n = 109	n = 109	n = 109	n = 208
Known females	151.4 ± 3.2	9.8 ± 0.8	2.2 ± 0.2	44.9 ± 1.7	72.7 ± 2.4	27.8 ± 2.5	22.9 ± 2.6
	(143.0–158.0)	(7.6–11.6)	(1.7–2.9)	(42.0–50.0)	(67.0–77.0)	(22.0–33.0)	(19.2–29.8)
	n = 44	n = 44	n = 44	n = 44	n = 44	n = 44	n = 44
Known males	153.1± 2.4	10.0 ± 0.7	2.2 ± 0.2	45.8 ± 1.7	73.9 ± 2.2	28.9 ± 2.6	22.5 ± 2.5
	(148.0–157.0)	(8.9–11.4)	(1.8–2.5)	(44.0–50.0)	(66.0–78.0)	(22.0–34.0)	(18.4–29.2)
	n = 35	n = 35	n = 35	n = 35	n = 35	n = 35	n = 35

Table 2. Results of the Principal Component Analysis on biometric measurements of Plain Swifts in Tenerife (Canary Islands). Tail exterior removed due to high correlation with fork.

	PC1	PC2
Wing	–0.93	0.14
Bill length	–0.09	–0.37
Bill depth	0.04	0.02
Tail interior	–0.01	0.65
Mass	–0.17	0.82
Fork	–0.65	–0.50
Eigenvalues	0.41	0.30
% variance	41.0	30.0

Identification of juvenile birds

Amongst the breeding birds, there were no difference in plumage or abrasion that could be used to separate birds into adult and first-years (breeding for the first time), so all birds caught were classed as adults. All juvenile Plain Swifts examined (n = 33) showed all flight feathers to be narrowly fringed with white along the inner webs (Fig 4). This feature first appears when chicks are 37 days old (see figures in Garcia-del-Rey 2006). The body feathers were distinctly browner than those of adults and fringed whitish, giving a scalloped effect, particularly noticeable on the crown, nape and rump. These features were first observed when chicks are around one month of age. The narrowly margined white on the outer web of T5 (exterior), an important characteristic for identifying juvenile Common Swift (Baker 1993) was not as visible as the fringes on the wing feathers.

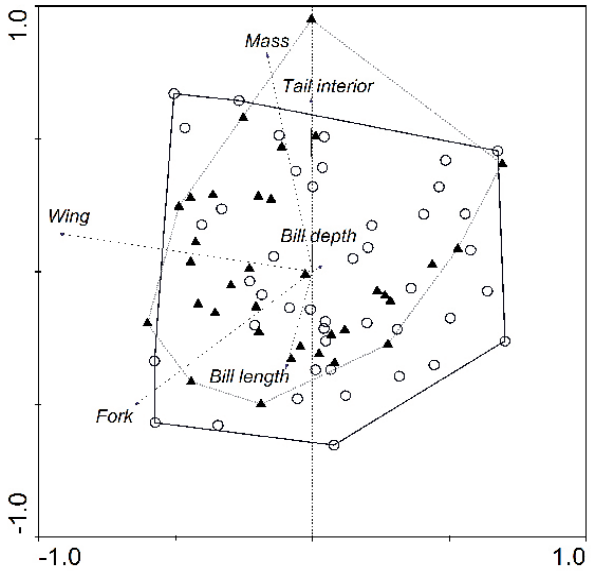

Figure 2. Principal Component Analysis of Plain Swift biometrics. Scores for the two principal axes are plotted (open circles = females, filled triangles = males) with 'envelopes' enclosing the values for males and females. The cumulative percentage of variance explained by axes 1 and 2 is 71.0%. The biometric variables appear as vectors (eigenvalue for axis 1: 0.41, eigenvalue for axis 2: 0.30.

Table 3. Logistic regression predicting sex based on wing length, bill length and tail (interior)

Predictor	B	Wald $\alpha 2$	*P*
Wing	–0.187	4.076	0.044
Bill length	–0.937	5.255	0.022
Tail interior	–0.464	6.757	0.009
Constant	58.992	11.394	0.001

Moult

During the course of this study, 30 adult birds were captured in various stages of primary moult between 17 August and 17 September (Table 4) and no moult was observed on 35 birds ringed on the 13 and 17 April. All moulting birds had started primary moult from the innermost primary (P1, numbered descendently as in Ginn & Melville 1983) but six birds (20%) had an irregular pattern of moult and had moulted P7 or P8 with concurrent growth of P1 to P3. The mean start date from maximum-likelihood estimation (Underhill & Zucchini 1988) from moult scores and data for the presence or absence of moult was 16 August ± 20

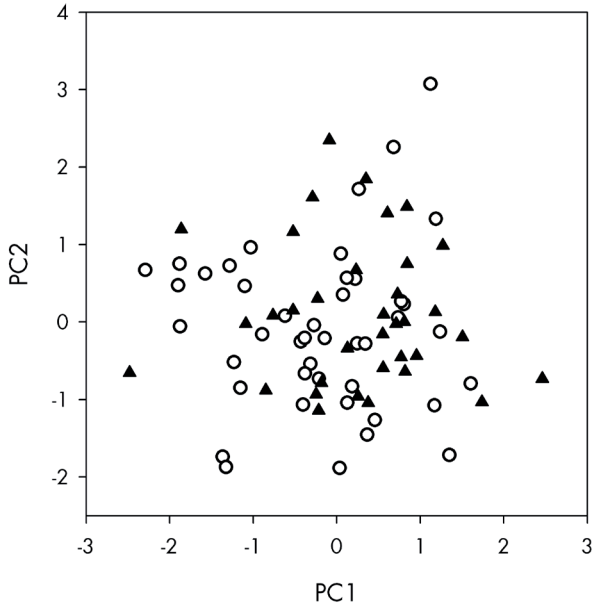

Figure 3. The placement of males (▲) and females (o) in the ordination space.

Table 4. Moult scores for primaries of 30 birds that were moulting when captured. Feathers are scored from 0 (old feather) to 5 (new fully grown feather) following Ginn & Melville (1983) and primaries are numbered descendently (*ie* P1= innermost).

	Primary									
	1	2	3	4	5	6	7	8	9	10
17 August	2	0	0	0	0	0	0	0	0	0
17 August	1	0	0	0	0	0	0	1	0	0
21 August	5	5	1	0	0	0	0	0	0	0
21 August	5	1	0	0	0	0	0	0	0	0
21 August	5	5	4	0	0	0	0	0	0	0
21 August	1	0	0	0	0	0	0	0	0	0
22 August	5	1	0	0	0	0	0	1	0	0
22 August	5	4	1	0	0	0	0	0	0	0
22 August	1	1	0	0	0	0	0	0	0	0
22 August	5	0	0	0	0	0	0	0	0	0
22 August	1	0	0	0	0	0	0	1	0	0
22 August	2	1	0	0	0	0	0	0	0	0
6 September	5	2	0	0	0	0	0	0	0	0
6 September	5	2	0	0	0	0	0	0	0	0
6 September	5	1	0	0	0	0	0	0	0	0
6 September	5	1	1	0	0	0	0	0	0	0
15 September	4	1	0	0	0	0	0	0	0	0
15 September	3	1	0	0	0	0	0	0	0	0
15 September	5	1	0	0	0	0	0	0	0	0
15 September	5	1	0	0	0	0	0	0	0	0
15 September	5	1	0	0	0	0	0	0	0	0
15 September	5	1	0	0	0	0	0	0	0	0
15 September	5	5	0	0	0	0	0	1	0	0
15 September	5	1	0	0	0	0	0	0	0	0
15 September	5	1	0	0	0	0	0	0	0	0
15 September	5	4	2	0	0	0	0	2	0	0
17 September	5	1	0	0	0	0	4	0	0	0
17 September	1	0	0	0	0	0	0	0	0	0
17 September	5	4	1	0	0	0	0	0	0	0
17 September	2	1	0	0	0	0	0	0	0	0

days (SD). Note that some birds (23.3%) were in active primary moult while still feeding young and seven birds regurgitated a bolus of insects when caught. The duration of moult could not be estimated as there were insufficient data for birds in the later stages of moult.

DISCUSSION

These results on sexual size dimorphism in the Plain Swift do not support previously published work based on skins (*eg* Cramp 1985), which stated that the species

Figure 4. A photograph of a nestling Plain Swift almost ready to fledge. Note the whitish fringe on the inner webs of the primary feathers.

is sexually monomorphic in size. The Plain Swift departs from monomorphism in at least two features: the lengths of the wing and tail (both interior and exterior measurements). According to the external measurement data based on skin specimens presented by Cramp (1985), of the seven breeding species in the Western Palearctic, four show significant sex differences (two species show sex differences in fork, one in wing and one in both of these measurements). However, for the other three species the sample sizes are small, and this included the Plain Swift. More recent work has shown similar results to the present study in the Alpine Swift *Apus melba* where males were slightly larger than females (P. Bize pers comm).

Body mass is an important measurement because, when taken with a measure of size (for example, wing length), it can give an indication of condition (Gosler *et al* 1998, Redfern & Clark 2001). Nevertheless, we should expect mass to increase with size, and we found no such correlation between wing length and mass, either within or between sexes, and only a weak correlation of mass with bill length. Hence, despite the sex difference in wing length, mass did not differ significantly between sexes. One explanation for this apparent lack of sexual dimorphism in body mass is that, during the breeding season, female mass may be increased relative to males due to the enlargement of the ovaries, which might not have regressed by the time that adults were captured. The period of sampling in the present study corresponded entirely with the breeding season of the swift. Most birds lay eggs ranging from 2% to 11% of body mass and swifts lay small eggs relative to their body masses (Gill 1995).

Our results suggest that modest sexual selection might operate in the Plain Swift and more detailed studies of coloration are needed. Although the Plain Swifts were

clearly dimorphic in size, the discriminant function was able to assign birds to sex with only 70% accuracy. Therefore, for future research, the routine use of blood samples for sexing in this species would be of considerable value. The inability of mass to contribute to the discriminant function for sexing was surprising, but it will be very difficult to investigate the use of mass data for sexing birds outside the breeding season because the birds become extremely erratic and difficult to catch after breeding (pers obs).

Although current knowledge of swift moult is limited, it is apparent that most migratory swift species time their moult cycles to coincide with arrival in the winter quarters, and this is achieved by starting primary moult on the breeding grounds and then suspending this until arrival in the wintering quarters, or by not beginning moult until the wintering grounds are reached (Chantler & Driessens 2000). However, we cannot rule out the possibility that, rather than suspending moult, Plain Swifts may have a slow progressive moult (which could take as long as six months), perhaps starting from more than one moult centre, as a flight-efficient strategy. Cramp (1985) suggested that the Plain Swift has a winter moult (*ie* adult post-breeding and post-juvenile) because none of 26 specimens examined between February and September was in active flight-feather moult. However, our results appear to contradict this, as we have found evidence that the moult cycle overlapped partially with the reproductive period in nearly 25% of the moulting birds. Considerable overlap between breeding and moult has previously been noted only in resident swifts, whereas the migratory species show no such overlap (Chantler & Driessens 2000). Therefore, the current moult data for Plain Swifts could be interpreted to suggest that the Plain Swift is a partial migrant in the Canary Islands, with part of the population staying, and another part leaving for wintering grounds elsewhere. Indeed, it is currently believed, but not proven, that part of the Canarian population departs to winter in North Africa (del Hoyo *et al* 1999). Further studies, perhaps using stable isotope analysis (*eg* Neto *et al* 2006), are needed to resolve this issue.

As in other *Apus* species (*eg* the Common Swift), juvenile Plain Swifts can be aged on the basis of differences in flight feather colour. All juveniles showed a narrow fringe of white along the inner webs of the primary feathers while sitting on the nest. However, no juveniles were captured after fledging and it is possible that, as in the Common Swift, this feature may be much reduced over the winter, giving first-winters a similar appearance to non-breeding adults. Studies on known first-year birds (second calendar year) ringed as chicks will be important to identify plumage criteria that can be used to age birds in the hand during the breeding season.

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