Seasonal Variation in Body Mass of Chimney and Vaux's Swifts

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ABSTRACT

Body mass of Chimney (*Chaetura pelagica*) and Vaux's (*Chaetura vauxi*) swifts is high early in the breeding season and peaks just before departure on fall migration. Mass is at a low during the breeding period and initiation of the annual complete molt. Premigratory gains in mass are not so large as in some migrant passerines, suggesting that fat reserves must be replenished at stopover points during migration .

INTRODUCTION

Information on the body mass of birds has considerable value in ecology, physiology, and even engineering (Clark 1979, Clench and Leberman 1978). Accordingly, useful compendia of avian mass data have been produced as by-products of 1) population studies involving banding (Collins 1972, Thomas 1979, 1990), 2) specimen collection (Hartman 1961, Olson and Angle 1977, Steadman et al. 1980), and 3) localized banding operations (Collins and Bradley 1971a, Clench and Leberman 1978). Comprehensive summaries of body masses are those by Dunning (1984) for North American birds and Brough (1983) and Dunning (1993) for birds of the world. In these summaries the emphasis has been on species coverage and, where sample sizes allowed, inter-sexual differences. However, many species also show extensive seasonal variation in mass, particularly migrants which characteristically accumulate substantial fat deposits prior to making lengthy migration flights (Blem 1976, Nisbit et al. 1963). Clench and Leberman (1978:4) report a 72% gain in weight of a Cape May Warbler (*Dendroica tigrina*) at a migratory stopover site. Detailed analyses of such seasonal variation have often been hampered by insufficient sample sizes or uneven seasonal coverage; an exception is the impressive analysis of 97,762 weights from 151 species banded at the Powdermill Nature Reserve in Pennsylvania (Clench and Leberman 1978).

As part of an investigation of body masses of swifts (Apodidae) and treeswifts (Hemiprocnidae) of the world (Collins and Marin in prep.), we present here an analysis of seasonal variation in the mass of two North American migrants: Vaux's Swift and Chimney Swift

METHODS

The data summarized here are derived from our recent field studies (Bull 1991, Bull and Collins 1993a, b, and unpublished), as well as several additional published and unpublished sources (Table 1). Data are presented as mean ± standard deviation and range. Bartlett (1952) and Dexter (1957a, b) indicate the absence of any significant sexual dimorphism in mass in Chimney Swifts. The absence of bimodality in several large samples of masses of Vaux's Swifts (this analysis) also suggests a lack of significant sexual dimorphism in this species. Thus, in this analysis, all data separated by sex (Fischer 1958, Johnston 1958) are combined and summarized, along with field data on unsexed birds, by half-month intervals (Table 1, Figure 1).

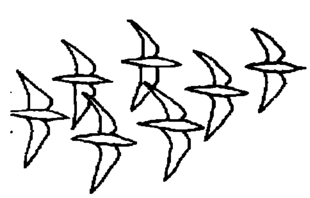


Table 1. Seasonal changes in body masses (g) of Chimney and Vaux's Swifts.						
Date	**Mean**	**SD**	**Range**	**N**	**Location**	**Source**
Chimney Swift						
March II	23.9	-	-	33	Tenn.	a
April I	22.9	-	-	33	Tenn.	a
April II	24.86	-	24.3-27	6	Georgia	b
May I	23.0	-	-	31	Tenn.	a
	23.75	-	-	6	Georgia	b
May II	24.9	4.3	20.0-27.0	72	Mass.	c
	24.45	1.39	21.5-28.0	119	Ohio	d
	25.38	2.6	18.4-26.8	12	New York	e
June I	22.9	-	21.6-24.5	6	Georgia	b
June II	22.8	-	21.8-24.3	3	Georgia	b
July I	20.8	-	-	7	Tenn.	a
	21.7	-	19.8-23.1	8	Georgia	b
August I	20.3	-	-	1	Georgia	b
	23.3	-	21.0-27.0	47	Ohio	f
August II	22.65	-	21.4-23.6	6	Georgia	b
Sept. I	21.67	-	-	309	Tenn.	a
Sept. II	20.37	-	-	854	Tenn.	a
	23.30	-	-	1	Georgia	b
	23.0	-	19.1-26.9	100	Kansas	g
October I	26.25	-	-	293	Tenn.	a
October II	30.1	-	28.3-31.7	5	Georgia	b
Sources: a (Coffey (1958), b (Johnston 1958), c (Bartlett 1952), d (Dexter 1957a,b), e (Fischer 1958), f (Stewart 1937, g (Cinc and Boyd 1979).						

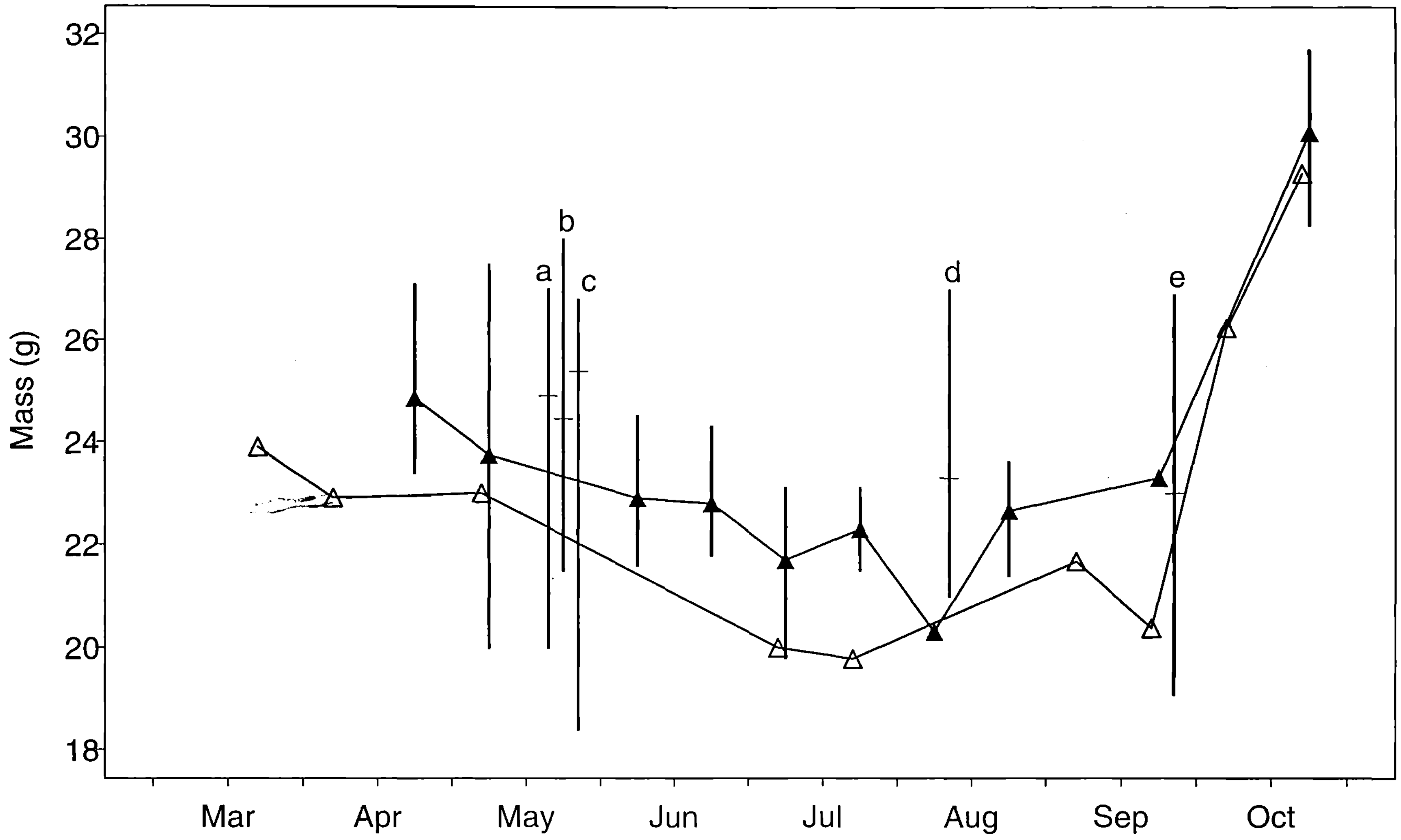
Table 1. Seasonal changes in body masses (g) of Chimney and Vaux's Swifts (Contd.)						
Date	Mean	SD	Range	N	Location	Source
VAUX'S SWIFT						
April II	15.41	-	14.1-17.4	35	So.Calif.	h
May I	14.93	-	11.5-19.8	36	So.Calif AM	i
	17.05	-	14.6-20.9	89	So. Calif PM	i
	19.45	-	16.7-27.5	40	Oregon	j
June I	-	-	-	-	-	-
June II	-	-	-	-	-	-
July I	18.33	-	16.4-22.0	16	E. Oreg.	k
July II	18.87	-	15.5-20.3	43	E. Oreg.	k
	17.23	-	16.4-19.0	4	Montana	l
August I	19.20	-	18.3-19.9	5	Montana	m
	18.24	-	15.5-20.6	52	E. Oreg.	n
August II	18.50	-	16.5-20.0	27	C. Oreg.	j
	19.97	-	17.7-21.6	64	E. Oreg.	n
Sept. I	20.12	-	17.8-22.6	25	E. Oreg.	n
	17.08	-	14.5-19.9	187	C. Oreg.	j
Sept. II	18.57	-	15.0-21.9	22	So. Calif.	0
Sources: h (Collins 1971), i (Wells and Nixon unpubl.), j (Payne unpubl.), k (Bull and Collins 1993a), l (Baldwin and Hunter 1963), m (Baldwin and Zackowski 1963), n (Bull unpubl), o (specimens, Natl. Hist. Mus. Los Angeles, Ca.).						

RESULTS

Chimney Swift — The largest single sample (n=1805) of body masses of Chimney Swifts (Dunning 1984, 1993) was obtained by Zammuto and Franks (1979) during the breeding season in Illinois. They reported a mean weight of 23.6 $\pm$ 0.3 (17.0-29.8 g) for adults. However, this summary value ignores the pattern of seasonal variation they illustrate (Zammuto and Franks 1979:Fig. 2) in which adults appear to average approximately 25 g in April, 21-22 g in July and August, and 23 g in early September. Data presented by Bartlett (1952), Coffey (1958), Dexter (1957a,b) Fischer (1958), Johnston (1958), and Stewart (1937) provide quantification of this pattern (Fig, 1, Table 1).

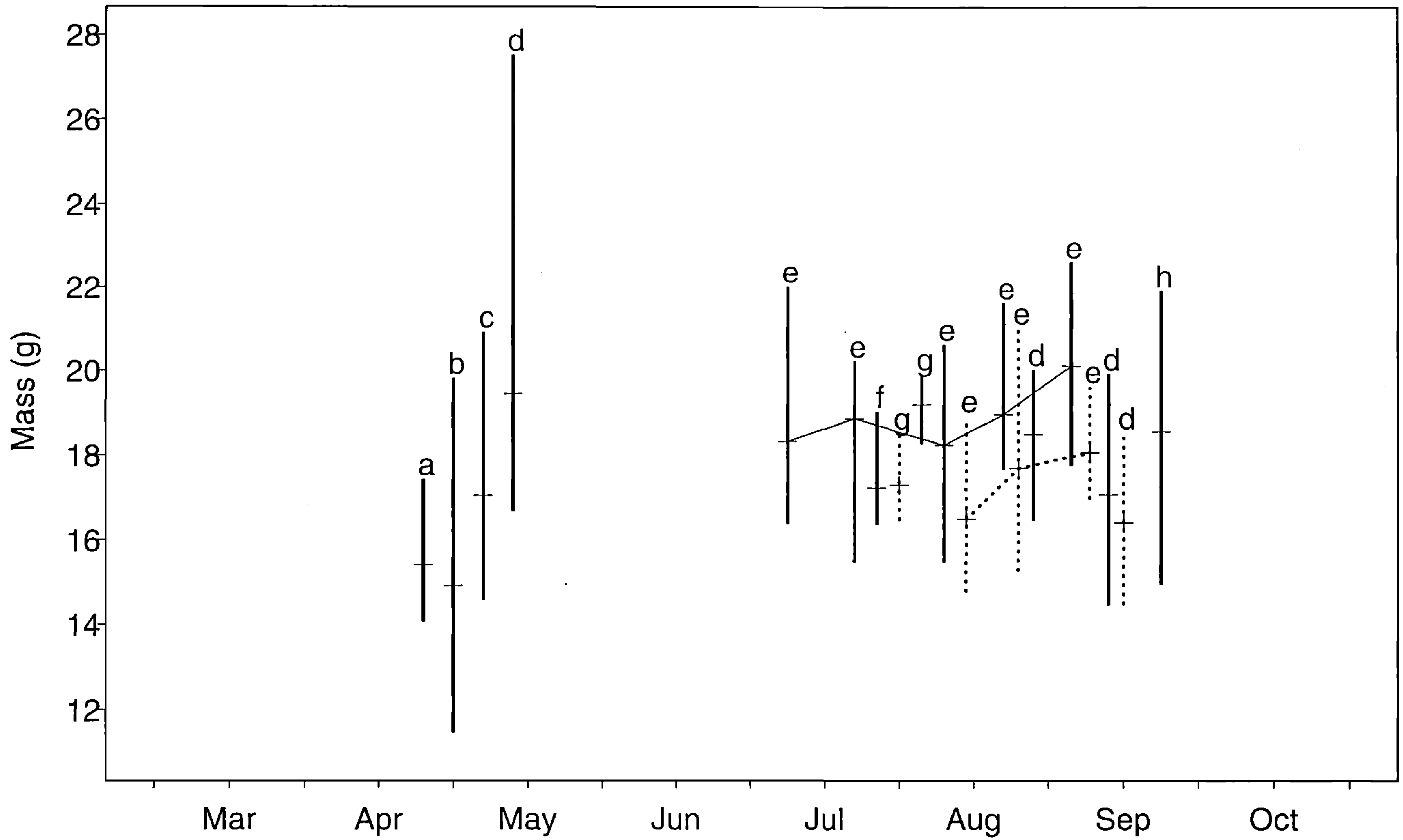
The overall pattern is similar to that indicated only graphically by Zammuto and Franks (1979); higher masses (23-25 g) are recorded from April to early June after which mass decreases to 19.5-23 g and remains at this level until a period of rapid gain in average mass to 26-30 g in early to late October (Table 1, Fig. 1). The data sets of Johnston (1958) and Coffey (1958) are similar in pattern but typically differ by approximately 1.5-2.0 g in magnitude (Fig 1.). These differences are probably due to differences in the time of day at which the data were collected. Coffey (1958)

Fig. 1. Seasonal changes in mean body mass of Chimney Swifts.



Sources: Solid triangles (Johnston 1958); open triangles (Coffey 1958); a (Bartlett 1952); b (Dexter 1957 a,b); c Fischer (1958); d (Stewart 1937); e (Cinc and Boyd 1979). Vertical bars indicate ranges.

Fig. 2. Seasonal changes in mean body mass of Vaux's Swifts.



Sources: a (Collins 1971); b (AM weights, Wells and Nixon unpubl.); c(PM weights, Wells and Nixon unpubl.);d (Payne unpubl), e (Bull and Collins 1993b, Bull unpubl.); f (Baldwin and Hunter 1963); g (Baldwin and Zaczkowski 1963); h (specimens, Nat. Hist. Mus. Los Angeles, Ca.). Solid vertical bars indicate adult ranges; dotted vertical bars indicate juvenile ranges.

weighed swifts early in the morning as they emerged from nocturnal roosts while Johnston (1958) obtained specimens late in the day "between 6 p.m. and dark" while the birds were approaching roost sites.

In light of these time-of-day differences, the early morning samples obtained by Bartlett (1952), Dexter (1957a,b) and Fischer (1958) in late May and early June are conspicuously heavy. These samples probably included more recently arrived residents and fewer passage migrants than may have been included in the other early season samples (Coffey 1958, Johnston 1958). If so, it would indicate that Chimney Swifts, upon reaching the breeding areas, are able to rapidly increase their body fat reserves expended during migration. These samples may have also included some egg-laying females but this cannot be examined further as most birds were not sexed. Thereafter, these reserves are apparently again expended, and mass decreases to an average of 22.3 g (21.5-24.5) during the breeding season (June-July: Johnston 1958) (Fig.1.) when they are feeding young and beginning the annual complete molt. The data reported by Stewart (1937) [determined by Fischer (1958:48) to have been collected in August] was somewhat higher but represented birds caught and weighed in the evening.

Post-breeding flocks containing molting adults show an increase in average body mass (Coffey 1958, Johnston 1958), particularly in October when large roosting flocks form in the southeastern states (Green 1940, Coffey 1958). This timing is just prior to the start of their transequatorial migration which includes a flight across the Gulf of Mexico (Lowery 1943) to wintering grounds in Peru (Plenge 1974) and Chile (Araya et al. 1972).

The information on body mass of migrating Chimney Swifts is anecdotal and conflicting. A single individual collected in Colombia on 8 April weighed 20.8 g (Miller 1963) and a single female collected in Belize on 24 March (Wood and Leberman 1987) weighed 24.0 g and was "moderately fat (specimen #102504, Carnegie Museum). In mid October, a flock of perhaps 200-300 migrant Chimney Swifts were physiologically trapped on the Islas del Cisne (the Swan Islands) 180 km north of Honduras. They apparently did not have the energy reserves (fat) to continue their southward flight and starved to death within a few days (Spendelow 1985). Forty freshly dead birds had an average weight of only 13.9 g (12.7-15.6) and were severely emaciated.

Vaux's Swifts - The overall pattern of seasonal body mass variation in Vaux's Swifts is similar, but not as clearly documented, as in the Chimney Swifts (Table 1, Fig. 2). An early season sample of roosting birds from the breeding range in Oregon (Payne, unpubl.; Table 2) is higher (19.44 g) than any late breeding season (July-August) samples (Bull and Collins 1993b, Table 2). This early season sample included one remarkable value of 27.5 g, which is 5 g more than any other recorded body mass for this species, and almost certainly represents an egg-laying female. While breeding, body mass of Vaux's Swifts decreases to 18.62 g (range: 16.4-22.0, Baldwin and Zaczkowsky 1963, Bull and Collins 1993a). Body mass of post-breeding adults at communal roosts on the breeding grounds in eastern Oregon increased to an average of 20.12 g shortly before the onset of migration in early September (Bull and Collins 1993b, Table 1). However, Vaux's Swifts at a large communal roost in central Oregon, at about the same date, averaged substantially lower (17.8 g ; Payne unpubl., Table 2); we do not know the weather conditions or the timing of departure at this site. A sample of birds obtained from a large flock at a migratory stopover roost in southern California had an average body mass of 18.57 g (Table 1). This frequently utilized roost, in Los Angeles, may have up to several thousand Vaux's Swifts using it over a period of weeks in September and October (K. Garrett, pers. comm.). Vaux's Swifts, overwintering in Florida, weighed 19.4 g at dusk (McNair and Lewis 1997) The body masses of migrating Vaux's Swifts in late April and early May (Wells and Nixon unpubl., Table 1), including some captured during a period of cold weather and headwinds (Collins 1971), are similarly lower (15.41-17.05 g) than breeding season levels. This difference is perhaps not unexpected if migrants rapidly expend their lipid resources.

Juvenile body mass — Zammuto and Franks (1979) give an overall value for body mass of 177 juvenile Chimney Swifts as 21.7 ± 0.7 g (18.3-26.2 g) but they also show graphically (1979; Fig. 2) that mass increases from approximately 19.5 g in July to near adult levels of 22-23 g in September. Coffey (1958) also found no significant difference between adult and juvenile masses in the post-breeding flocks trapped in September and October.

Juvenile Vaux's Swifts in eastern Oregon had an average body mass of 17.3 g in July which increased to 18.1 g in early September prior to migration (Bull and Collins 1993a,b, and unpublished) (Fig. 2). At this time they still averaged 2.05 g less than the adults.

Molt— Molt in birds is generally considered to be one of the major energetic expenditures in the annual cycle (Gill 1990) and would thus influence stored energy reserves (fat) and mass. The annual complete molt of adult Chimney Swifts begins with the loss of primary number one in early June (Johnston 1958) and ends with the replacement of primary 10 between the middle of September and early October (Coffey 1958, Johnston 1958). In Vaux's Swifts, in Oregon, primary molt was calculated to begin in late June and finish in mid October (Bull and Collins 1993a,b). As in other *Chaetura* swifts, the period of primary molt generally encompasses the period of rectrix and contour plumage molt (Collins 1968; pers. obs.) and overlaps broadly with breeding. The energetic cost of molt, along with chick rearing, may contribute to the low mass recorded in these swifts in mid-summer.

DISCUSSION

In both the Chimney and Vaux's swifts mass seems greatest in the fall just prior to migration when the birds are usually found in large communally roosting flocks. There is some indication that mass is also high in pre-breeding birds which have recently reached the breeding grounds. Mass is usually substantially lower in migrating Vaux's and Chimney swifts, suggesting that in both species body fat reserves are rapidly expended during migration and need to be replenished en route. Neither species appears to accumulate the very high level of fat reserves found in some long distance or intercontinental migrants (Blem 1976, Nisbit et al. 1963) and which would be necessary to make long non-stop flights. Chimney Swifts only increase body mass by 34% and Vaux's Swifts by 8% in the postbreeding period. For both species, lengthy stays at migratory stopover points may be necessary to replenish energy reserves. This is particularly true for the Chimney Swift which is a trans-gulf migrant in spring and fall (Lowery 1943). Large aggregations of Chimney Swifts have been reported at such stopover locales. Body mass appears to be lowest during the breeding season when chick provisioning and molt place additional energy demands on the breeding adults.

Studies of the Common Swift (*Apus apus*) have documented this same pattern of change in body mass (Lack and Lack 1951, Gladwin and Nau 1964). Martins and Wright (1993) found that breeding adult Common Swifts have largely exhausted their stored fat reserves during the chick-rearing period and must allocate some of their food energy acquisiton to meeting their own needs, even at the expense of the demands of their growing young.

In this analysis it has been largely assumed that most of the observed changes in body mass are related to the deposition and utilization of lipid reserves. Support for this view is presented by Johnston (1958), who noted that the seasonal change in mass he observed in Chimney Swifts was "believed to be correlated closely with fat deposits." His subjective observations were that "birds taken in April ....were 'moderately fat', those taken in June had 'no fat', and those taken in July and August had 'some fat'. The few birds collected in October were termed 'very fat'." Zammuto and Franks (1979:Table 3) similarly estimated visual fat reserves of Chimney Swifts to be high in early May, lower in mid-summer and again high in the premigratory period. In a small sample of fall migrant Vaux's Swifts collected in southern California (Table 2; specimens, Natural History Museum of Los Angeles County) some of the lightest specimens were noted to have "light fat" or "no fat" while some heavier specimens were noted as being "very fat." As would be expected in aerial foraging birds, only in extremely emaciated and starving Chimney Swifts were there signs of severe pectoral muscle atrophy (Spendelow 1985).

Overnight loss in mass has not been documented in these swifts, but body masses are clearly higher in the evening (Johnston 1958) than early in the morning (Coffey 1958) at the same season of the year. Diurnal weight loss of non-flying, presumably post-absorptive, captive Chimney Swifts averaged 0.16 g/hr (Zammuto and Franks 1979) and 0.21-0.28 g/hr (calculated from Coffey 1958). Overnight loss in mass of a Vaux's Swift was 0.12 g/h (McNair and Lewis 1997). Gain in mass in one day for free-flying Vaux's Swifts averaged 2.12 g when comparing two samples of presumably the same group of spring migrants weighed at dawn and in the evening after roosting (Wells and Nixon unpubl., Table 2). Recovered individuals reweighed on both occasions (n=10) only gained 0.74 g (0.1-1.3 g) during the same interval. The difference may reflect some degree of handling shock which resulted in an initial loss in body mass in migrant thrushes (Collins and Bradley 1971b, Mueller and Berger 1966).

Body mass of Chimney Swifts captured on two or more occasions were not the same (Coffey 1958, Fischer 1958). However, the differences were generally small, averaging about 3%; 22 swifts weighed on two or more occasions in the same season showed an average change in mass of 0.71g ± 0.71 (0.0-1.8) (Fischer 1958). Differences in mass of four individuals weighed in different years averaged 0.87 g (0.2-1.6) (Fischer 1958).

In 35 cases of Vaux's Swifts captured on the breeding grounds, individuals weighed on two or more occasions in the same season showed an average change in mass of 1.08 g ± 0.8.8 (0.0-4.1) (Bull unpubl.). In 33 cases of adult Vaux's Swifts weighed in different years the average difference in mass was 1.05 g ± 0.72 (0.0-2.5). A non-migratory population of Vaux's Swifts in northern Venezuela (*C. v. aphanes*) had a mean body mass of 18.11 g ± 1.2 (15.25-22.0; n=174) (Collins 1972) and a similar variation (0.68g ± 0.55 [0.0-1.75]) in weights of eight individuals weighed more than once during the same season.

The timing and duration of molt in birds are both flexible and highly adaptive. Typically the annual complete molt follows breeding and precedes migration with few species breeding and molting at the same time (Gill 1990). Exceptions include some tropical species which exhibit overlap of molt and breeding (Foster 1975, Payne 1969). In both temperate and tropical *Chaetura* swifts there is substantial overlap of breeding and the annual molt (Collins 1968). Swifts' dependence on aerial foraging presumably limits the number of flight feathers which can be in molt at any one time. This would account for the prolonged duration of their annual molt (about 108 days in Vaux's Swifts; Bull and Collins 1993a) and its broad overlap with breeding and timing so that it occurs between periods of migration. This is presumably also the season of maximum food availability. An alternate strategy, utilized by European populations of the Common Swift, is to delay the annual molt until after the fall migration when they have reached the wintering ground in central Africa (DeRoo 1966).

Further analyses of the seasonal changes in body mass of other species of birds, including both migratory and resident species or populations should be undertaken. The results should enhance our understanding of the annual pattern of energy availability and the adaptive utilization of it by birds.

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