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The Condor 99:538–543
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FAT LOADS AND FLIGHTLESSNESS IN WILSON'S PHALAROPES¹

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Abstract. Fat loads of about 45% of total body mass are maximal for most shorebird migrants. In preparing to fly nonstop from staging areas in North America to South America, some late-staging adult Wilson's Phalaropes (*Phalaropus tricolor*) amass greater loads (to 54%) and for a brief period become too heavy to fly. This condition is associated with rapid mass gain, but may involve other factors. Despite os-

tensibly ideal conditions at staging areas, the phalaropes' greatest rate of fat deposition (3.4–3.6% lean body mass-day⁻¹) is only 60–70% of the theoretical maximum.

Key words: *Wilson's Phalarope*, *Phalaropus tricolor*, *migration*, *energetics*, *fat*, *flightlessness*.

Except for periods associated with the loss of remiges, as in the molt migration of waterfowl or other birds (Salomonsen 1950, Jehl 1990), the loss of flying ability is very rare among volant birds. The most extreme

¹ Received 1 August 1996. Accepted 8 December 1996.

case yet documented occurs in the Eared Grebe (*Podiceps nigricollis*) at fall staging areas, where individuals may be flightless for six months or more because of atrophy of pectoral muscles (Jehl 1988, 1997, Gaunt et al. 1990). Wilson's Phalarope (*Phalaropus tricolor*) provides another example. After the breeding season, adults move to hypersaline lakes in the Great Basin of the western United States where they stage for 5–6 weeks and prepare for the next stage of the migration. In the first half of this staging period the birds undergo a major and rapid molt in which they replace most of the body plumage, rectrices, and several primaries (Jehl 1987, 1988). In the second half, after the molt has largely been completed or is arrested, they become hyperphagic and fatten in preparation for a non-stop flight to northern South America. At the end of the staging period, when the birds are obese and on the verge of departing, some become flightless for a brief period (Jehl 1988, Colwell and Jehl 1994), the duration of which has not been established. The scheduling of this event suggests that it is related to physiological changes, and specifically the fat load amassed by birds prior to the start of a long (≈ 60 hr) non-stop flight. If so, then better understanding of this phenomenon is relevant to understanding the energetics and limitations of long-distance migrants.

METHODS

In the course of long-term studies at Mono Lake, California (1980–present), I have observed flightless phalaropes almost annually, but only among adults, which comprise virtually all (> 98%) of the Wilson's Phalaropes that stage at Mono Lake (Jehl 1988). To clarify the basis for flightlessness and the conditions that might cause it, I reviewed data on the body condition of Wilson's Phalarope migrants (Jehl 1988, unpubl. data, Ellis and Jehl 1991), including my field notes on the occurrence and behavior of flightless birds. During this project I had captured, weighed, and released hundreds of phalaropes, and also collected representative samples through the staging period for information on molt, body condition and migration. Nearly all of that information pertained to volant birds. To obtain data on the body condition of flightless birds for the present study, I supplemented the earlier samples by shooting or dip-netting small numbers of birds considered to be flightless, viz., those that either could not or would not fly when approached closely (< 5 m) by boat. Specimens were obtained between 10:00 and 12:00, dried to constant mass to determine water content, then ground up and immersed in petroleum ether to determine fat content (for details see Ellis and Jehl 1991). In this paper, I define fat load as a percentage of total body mass [fat (g)-wet weight (g) $^{-1} \times 100$] rather than lean body mass (cf. Gudmundsson et al. 1991). This is the most pertinent index to flight capability because (1) as a fraction of total body mass, fat load incorporates information about nonfat components which are not held constant as birds prepare to migrate [typically they increase (e.g., Lindström and Piersma 1993), but they also can decrease (Jehl 1997)], and because (2) the upper limit to the amount of fuel that can be transported is a function of wing-loading and, therefore, total body mass.

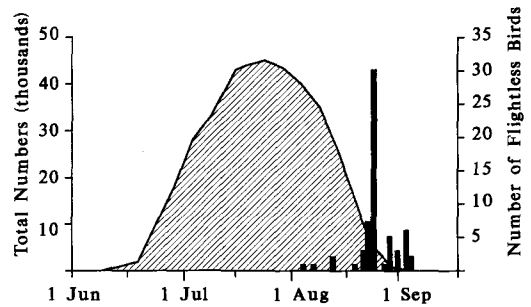


FIGURE 1. Typical pattern of timing and abundance (hatched area) of Wilson's Phalaropes staging at Mono Lake, CA, in the 1980s. Solid bars indicate numbers of flightless individuals.

RESULTS

BEHAVIOR, TIMING, AND ABUNDANCE

Early in the staging period, when phalaropes are molting intensively, their daily movements mainly consist of flying between feeding areas on the lake and shoreline roosts (Jehl 1988). At dusk they fly well offshore to roost overnight on the water. In the latter half of the staging period, when they are doubling body mass in preparation for migration, they become so obese (see Fig. 35, in Jehl 1988) and clumsy that they can no longer walk along the beaches, and some, at least, become too heavy to even stand on dry land (Jehl 1988, Colwell and Jehl 1994). Consequently, they abandon any pretense of being "shorebirds," become increasingly "pelagic," and eventually spend virtually all of their time on the open lake.

Over most of the staging period Wilson's Phalaropes are shy and flush straight into the air when a boat approaches within 50 m. Late in the season, however, their behavior changes. Birds that are obviously obese become reluctant to fly and can get airborne only after making a long run over the water, and some are unable to take off at all. Although an occasional bird will become flightless during the main departure period (1–15 August), nearly all of my sightings of flightless birds have come in the latter half of August, well after 90–95% of the adults have left (Fig. 1). Even then, the numbers involved are very small, the highest single daily count was 29 (1%) captured from a population of 2,400 on 23 August 1995, only 12–36 hr before half of that flock emigrated.

FAT LOADS AND RATE OF FATTENING

Obesity is clearly associated with flightlessness because flightless birds tend to have high fat loads (36.7–54.4%, $\bar{x} \pm SD = 49.0 \pm 4.7$, $n = 13$; Fig. 2) and are near the top of the mass range for the species (35 flightless males, range 77.5–105 g, $\bar{x} = 94.4$ g; 10 flightless females, range 91–131 g, $\bar{x} = 119.1$ g; 15 unsexed birds, range 85–115 g, $\bar{x} = 100.8$ g (for larger samples of masses of volant birds see Jehl 1988). Both fat loads ($\bar{x} \pm SD = 49.7 \pm 3.4$) and body masses (93.4 ± 7.0 g, $n = 10$) of flightless males in the period 13 August–1 September were significantly higher (t -tests, $P_s < 0.05$) than those of volant males (fat load

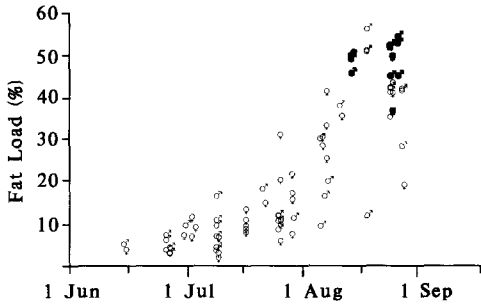


FIGURE 2. Temporal variation in extracted fat loads (% total body mass) in Wilson's Phalaropes staging at Mono Lake, CA. Filled points represent flightless individuals.

= 40.2 ± 12.1 ; body mass = 82.5 ± 13.5 g; $n = 11$). Flightless females ($n = 3$) were fatter ($\bar{x} = 45.7\%$) and heavier ($\bar{x} = 127.9$ g) than volant females ($n = 3$, $\bar{x} = 34.5\%$ and 100.6 g, respectively), but the differences were not significant because of small sample sizes. In addition, a high rate of fattening is suggested because both fat load and body mass (Fig. 3) increased exponentially as phalaropes neared peak mass. Given a mean lean body mass (LBM) of 47.8 g in males and 62.2 g in females (Jehl, unpubl. data), and following Lindström (1991), I estimate the maximum rate of fattening among late-staging females (mass increasing from 70 – 130 g between 25 July and 19 August) at 3.56% LBM-day⁻¹, and for males (mass increasing from 61 – 105 g between 28 July and 22 August) at 3.43% LBM-day⁻¹.

DISCUSSION

POSSIBLE CAUSES OF FLIGHTLESSNESS

Salt encrustation. In highly saturated environments, as at some waste disposal ponds, waterbirds can become salt-encrusted and incapable of flight within a few hours (Meteyer et al., unpubl. data; pers. observ.). This condition has not been observed at Mono Lake [total dissolved solid (tds) ≈ 85 – 100 g L⁻¹] or other hypersaline lakes of the Great Basin (e.g., Great Salt Lake, tds > 200 g L⁻¹), where phalaropes maintain good feather condition despite high salt concentrations.

Molt. Wing molt is not involved. Phalaropes molt up to 6 primaries at staging areas, but replace them completely before departing (Jehl 1987, 1988). Flightless birds are invariably full-winged.

Gorging. Because prey populations are superabundant at Mono Lake in the staging period, one might posit that flightless phalaropes are simply individuals that have eaten so much during their hyperphagic stage that they have been rendered temporarily flightless by the mass of food contained in their gut, as sometimes occurs in eiders (Guillemette 1994) or scavenging procellariiforms and vultures. This seems unlikely, however, because the gizzard contents of flightless phalaropes are much lighter, averaging only about 30% as heavy as those of volant birds entering the hyperphagic stage (flightless: $n = 7$, $\bar{x} = 0.30$ g, range 0.23 – 0.42 g; volant $n = 8$, $\bar{x} = 1.04$ g, range 0.47 – 1.27 , $P <$

0.01). Furthermore, three phalaropes kept overnight in a dark box remained unable to fly and swam off when liberated 16 hr later. Another released immediately after banding was flightless—and presumably had been so continuously—when it was re-netted 24 hr later, having lost 3 g of body mass. If gorging, alone, had been involved, these birds should have regained flying condition as soon as their gut contents had been digested.

Obesity. The most likely explanation is that hyperphagic Wilson's Phalaropes lay on fat so rapidly that they overshoot the optimal fuel reserves needed for long-distance migration, as well as the maximum wing-loading allowable for flight. Whereas the idea may seem hard to accept for healthy adult birds, several attributes of Wilson's Phalarope biology make it plausible: (1) they use open water habitats where (2) food is widely available and can be accessed entirely by swimming, and (3) where the risk of predation is minimal. In addition (4) food is superabundant at the lakes at which they stage. As a result, some individuals may not need to fly daily to seek food or safety. Even casual scrutiny of flightless birds leaves little doubt that their condition is associated with obesity; note, too, that birds that are technically volant also have great difficulty in flying just before migrating and need long coot-like dashes along the surface to attain flight.

According to Alerstam and Lindström (1990) rates of fat deposition in a variety of shorebirds (evidently calculated over an entire staging period) average 1.3% LBM day⁻¹. Estimated peak rates of fat deposition for individual Wilson's Phalaropes late in the staging periods are considerably higher (3.26 – 3.55%), yet remain 30 – 40% below the theoretical maxima [determined by Lindström (1991) as 5.39% in males and 5.02% in females]. Although this may be great enough to render them flightless, the "low" rate is surprising because phalaropes stage in an environment that is thermally neutral and where food is so abundant that birds need not forage continuously (pers. observ.), and because fattening phalaropes seem to employ behaviors (remaining offshore, reduced flying, arrested molt) that would minimize daily energy expenditure. Perhaps the rate of fattening at Mono Lake is limited by the relatively low caloric value ($4,413$ cal g⁻¹; Herbst et al.

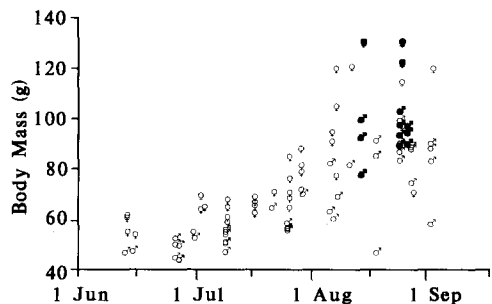


FIGURE 3. Temporal variation in body mass in Wilson's Phalaropes staging at Mono Lake, CA. Filled points represent flightless individuals. For additional data on body mass see Jehl 1988, Figure 36.

1984) and poor digestibility of brine shrimp (*Artemia monica*), which are the phalaropes' major prey during the fattening phase (Jehl 1988). The assimilation efficiency for other species that feed on these highly-sclerotized crustaceans is about 50% (Bryant and Bryant 1988), a figure likely to be too high for phalaropes at Mono Lake because 38% of a female shrimp's mass in the fall consists of encysted eggs (R. Jellison, pers. comm.), which are difficult to digest (Castro et al. 1989). If greater rates of fattening are attainable, it might be at Great Salt Lake where phalaropes feed mainly on brine flies (*Ephydra* sp.), which occur in incredible abundance, have an energy content 10–20% greater than brine shrimp on a per gram basis (Herbst et al. 1984), and are more easily digested (assimilation efficiency ~75%; Karasov 1990; see also Kersten and Piersma 1987, who estimated assimilation efficiency in shorebirds at 85%). I have never encountered flightless phalaropes at Great Salt Lake, but this probably reflects my limited boat-based observations at the critical period, rather than the absence of the phenomenon.

If obesity and rapid fattening were the only factors affecting flightlessness, however, large numbers of flightless birds of either sex should be seen throughout the species' entire departure period, starting as soon as the earliest migrants attained peak mass and prepare to leave. Instead, only a few birds are involved, and most of these are males, because the phenomenon occurs almost entirely at the very end of the migration period after most females have left (Jehl 1988). Furthermore, there are exceptions. A few nonfliers not only are lighter than fliers but also are below the estimated minimum mass needed to reach the wintering areas (≈ 85 g in males and 105 g in females; Jehl 1988); one of these, a very light and apparently uninjured male, weighed only 58 g 8 hr after being captured. By contrast, some fliers have greater fat loads than nonfliers (Fig. 2).

Timing is probably one key to understanding this event. I suspect that phalaropes that become flightless are those that have arrived late at staging areas (perhaps after having attempted a second clutch?; references in Colwell and Jehl 1994) and are trying to synchronize their schedules with that of the main population, which has already departed. This requires them to add fuel as quickly as possible, which in turn requires that they minimize daily energy expenditure. Thus, late-arriving migrants suspend wing molt (Jehl 1987) and spend their entire time on the open lake where food is abundant and flight may be unnecessary. But this idea, while accounting for obesity, does not explain why so few late migrants take this option. In Eared Grebes, pectoral muscles can begin to atrophy in migrants that have been downed and grounded for only a day or so (Jehl 1988, 1994, Gaunt et al. 1990). Perhaps phalaropes also need to exercise regularly to maintain their flight muscles, and those that neglect to fly while gorging for several days find themselves weakened and stranded temporarily, until muscle tone can be regained.

As noted above, I have never found flightlessness among the few juvenile phalaropes that stage at Mono Lake. This reflects their different migration pattern. Juveniles in general do not concentrate at the major stag-

ing lakes and ultimately migrate to South America by using a series of short flights, rather than a single over-water crossing. As a result, they do not accumulate the huge fat reserves that characterize adults in the fall (Jehl 1988).

FAT LOADS AND FLIGHTLESSNESS IN OTHER SPECIES

The observation that fat loads limit flying ability in Wilson's Phalaropes is relevant to the broader question of how much fuel a bird can carry at the start of migration. In shorebirds studied at terminal staging areas, peak loads of 40–45% seem to be typical (Table 1). These are probably near maximal because although individuals that can fly only with great difficulty are sometimes observed [e.g., Ruddy Turnstone, *Arenaria interpres* (M. Thompson, pers. comm.); Red Knot, *Calidris cautus* (B. Harrington, pers. comm.); Dunlin, *Calidris alpina* (R. Gill, pers. comm.); Bristle-thighed Curlew, *Numenius tahitiensis* (J. Marks, pers. comm.); Semipalmated Sandpiper, *Calidris pusilla* (P. Hicklin, 1987, and pers. comm.)], flightlessness is virtually unknown. Only one of the above authorities (Hicklin), each with multi-year experience involving thousands of birds, reported *once* seeing a *single* Semipalmated Sandpiper that could be captured afoot. Thus, obese and flightless Wilson's Phalaropes, with fat loads averaging about 49%, like pre-migrant Eared Grebes, evidently stop eating, as indicated by their minimal stomach contents, and burn off excess fat before they can regain flying ability and achieve optimal migratory condition (Gudmundsson et al. 1991, Jehl 1997). Eared Grebes also greatly reduce the size of their viscera, presumably to reduce wing-loading (Jehl 1997). Whether phalaropes or other long-distance migrants employ this as a mass-reduction mechanism deserves further investigation.

That typical shorebirds rarely, if ever, become flightless is hardly unexpected. Strand-foraging birds must move frequently to find food and avoid predators and, unlike the aquatic Wilson's Phalarope (or molting waterfowl), cannot risk periods of flightlessness. The Red-necked Phalarope (*Phalaropus lobatus*) also occurs commonly at Great Basin lakes in fall, and it spends nearly all of its time in open-water. However, it does not use these lakes as terminal staging areas and does not lay on the extreme fat loads that characterize long-distance migrants (maximum 30.9%; Jehl, unpubl. data). There are no reports of Red-necked Phalaropes becoming flightless (Jehl 1986, unpubl. data) or exhibiting difficulty in flying.

I thank S. Bond, H. Ellis, D. Jehl, J. D. Jehl, M. Messersmith, and J. Terp for assistance in the field, B. Harrington, R. Gill, P. Hicklin, J. Marks, T. Piersma, and M. Thompson for use of unpublished data or observations, and R. C. Banks, P. C. Rasmussen, H. I. Ellis, R. Gill, T. Piersma, B. Livezey, and several reviewers for thoughtful comments on the manuscript. This research was supported in part by the Los Angeles Department of Water and Power.

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TABLE 1. Some fat loads of long-distance shorebird migrants at terminal staging areas.

Species	Locality	Destination	Fat load (% wet wt.)	Comments/source
<i>Calidris canutus</i>	West Germany (Wadden Sea)	Siberia	\bar{x} = 36.0 ^a (n = 48)	Recalculated from Gudmundsson et al. 1991 (Table 1)
	SW Iceland	NE Canada	\bar{x} = 35.4 ^a (n = 12)	Same as above
<i>Calidris alba</i>	England		\bar{x} = 40.1 ^a (n = 29)	Recalculated from Gudmundsson et al. 1991 (Table 2)
	SW Iceland	NE Canada Greenland	\bar{x} = 34.6 ^a (n = 36)	Same as above
	Southern Africa	Mediterranean region	41–44 \bar{x} = 43.2 ^b (n = 4)	Peak loads in spring; Summers et al. 1987
<i>Arenaria interpres</i>	SW Iceland	NE Canada	\bar{x} = 42.1 ^a (n = 55)	Recalculated from Gudmundsson et al. 1991 (Table 3)
<i>Calidris alpina</i>	Alaska	Pacific coast U.S.	\bar{x} = 41.8 ^b (n = 66)	R. Gill, pers. comm.
<i>Numenius tahitiensis</i>	Laysan Is. (Hawaii)	Alaska	36.3–47.0 ^b \bar{x} = 42.5 (n = 6)	Marks and Redmond 1994
<i>Pluvialis fulva</i>	Hawaii	Alaska	25.4–36.8 ^b \bar{x} = 32.3 (n = 13)	Johnson et al. 1988
<i>Calidris pusilla</i>	Bay of Fundy, Canada	N. South America	\bar{x} = 40.0 ^b (n = 31)	Hicklin 1987
	Ontario, Canada		42.1 ^b , 50 ^c (n = 53)	Page and Middleton 1972
<i>Phalaropus tricolor</i> (flightless)	Mono Lake, CA	South America	36.7–54.4 ^b \bar{x} = 49.0 (n = 13)	This paper

^a Estimated as function of assumed lean body mass.

^b Based on extracted fat.

^c Maximum estimated load.

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The Condor 99:543–548
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RELATIVE COSTS OF PREBASIC AND PREALTERNATE MOLTS FOR MALE BLUE-WINGED TEAL¹

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Abstract. We compared masses of definitive basic and alternate plumages of male Blue-winged Teal (*Anas discors*) to evaluate the hypothesis that nutritional investments in basic and alternate plumages are related to the duration that plumages are worn and to assess the relative costs of prebasic and prealternate molts. Because these plumages are worn by males for approximately equal durations, we predicted that masses of the basic and alternate body plumages would be similar. To assess nutritional stress (demands greater than available resources) associated with molt, we examined the relation between remigial length and structural size and compared predicted and observed plum-

age masses of Blue-winged Teal and other ducks. If birds were nutritionally challenged during remigial molt, then we predicted remigial length would be influenced by nutrition rather than size, and remigial length and size would be unrelated. Alternate body plumage of male Blue-winged Teal weighed about 10% more than the basic body plumage; however, masses of both plumages were less than that predicted on the basis of lean body mass. We argue that deviations between observed and predicted plumage masses were related to factors other than nutrition. Further, remigial lengths were significantly, albeit weakly, related to structural size. We therefore concluded that, although the potential for molt-induced stress may be greatest in small-bodied waterfowl species, there was no clear evidence that molting male Blue-winged Teal were nutritionally stressed.

Key words: *Anas discors*, *Blue-winged Teal*, *Anatidae*, *molt*, *nutrition*, *plumage*, *stress*.

¹ Received 17 September 1996. Accepted 28 January 1997.

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