

MIGRATION AND BIOENERGETICS OF FLIGHT IN THE PACIFIC GOLDEN PLOVER

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Many migratory birds undertake long-distance, nonstop flights over vast expanses of water. Such flights have attracted the attention of ornithologists for many years, but only recently have intensive attempts been made to understand related phenomena such as navigation and the energy requirements of migratory flight. The recent literature contains several reports of studies of lipid reserves in migrant passerines, and other papers have dealt with flight-distance estimates and flight-energy requirements. One of the earliest observational studies of long-distance migrants among shorebirds was that of Henshaw (1910) on the Pacific form of the Golden Plover, *Pluvialis dominica fulva*. Henshaw pointed out that these birds perform overwater flights of about 2400 miles between Hawaii and Alaska. We have had the opportunity in recent years to study this species on Wake Island, and in the present report attention is focused principally on the special energy requirements of the plovers migrating to and from this island.

Wake Island is a coral and shell atoll in the northern Pacific Ocean (lat 19° 17' N, long 166° 39' E). It consists of three small, contiguous islets arranged in a "V" shape atop the rim of an extinct volcano and encircling a triangular lagoon. The total land area of the atoll is less than three square miles; average elevation above sea level is 12 feet, the maximum elevation being 20 feet. The island is comparatively isolated, the nearest landfall being Taongi Atoll, 375 miles to the south. Eastward are Johnston Atoll (1600 miles) and Midway Atoll (1200 miles). To the west are Marcus Island (900 miles) and the Mariana Islands (1400 miles).

Several species of migrating shorebirds stop on Wake Island, and some of these, especially the Golden Plover, winter on the island. During seven visits (ranging from 9 to 23 days each) between June 1963 and May 1965 we have observed the movements, numbers, and ecology of the migratory avifauna. Our objectives have been (1) to obtain data on migratory movements of the plovers, (2) to collect representative samples in different seasons for carcass analysis, (3) to relate molt and morphologic features to migratory movements, (4) to obtain basal rates of metabolism from captive plovers, and (5) to estimate flight-distance capabilities of plovers based upon our knowledge of lipid levels, flight speed, and basal rates of metabolism. Our samples, all collected in 1964, included 27 birds from April, 11 from August, and 12 from December.

For details of the technique of carcass analysis, see Johnston (1962, 1964). Basal rates of metabolism were determined by measuring the oxygen consumption of two plovers netted on Wake Island and transported to our laboratories at the University of Florida. Oxygen consumption was measured with the use of a Beckman paramagnetic oxygen analyzer, model F3.

GEOGRAPHIC DISTRIBUTION OF THE PACIFIC GOLDEN PLOVER

The breeding range of the Pacific form of the Golden Plover extends from the tundra of the Yamal Peninsula eastward across northern Siberia to western Alaska, where it occurs along the coast from Cape Lisburne south to the Kuskokwim River (for details see Sauer, 1962, and Vaurie, 1965). It winters throughout Oceania and the Oriental Region, west to Africa (from Somaliland to the Cape of Good Hope;

see Rudebeck, 1963), and as far south as Australia, New Zealand, and the Tuamotu Archipelago.

Golden Plovers on Wake Island are believed to migrate to and from their breeding grounds in the Arctic by a direct overwater route to the Aleutian (Murie, 1959) and Commander islands and the Kamchatka Peninsula and thence on to western Alaska and eastern Siberia. No direct evidence of this route is available, however, because there have been no recoveries yet of the plovers banded on Wake Island or in the Alaskan region. Plovers leaving Wake in the spring could go northeastward to Midway, although this route appears unlikely to us because of prevailing winds. However, Ruddy Turnstones (*Arenaria interpres*) banded in the Pribilof Islands have been recovered 13 to 40 days later from the Marshall and Caroline islands, lying south and west of Wake (Max Thompson, personal communication). This species frequently accompanies Golden Plovers on Wake.

All the plovers obtained on Wake Island are referable to the Pacific race, *P. d. fulva*, on the basis of wing length and coloration.

HABITATS ON WAKE ISLAND

Wake Island has several habitats frequented by shorebirds (for details of habitats, see Bryan, 1959 and Fosberg, 1959). Large areas at the apex of the triangular lagoon are exposed at low tide. These flats of bare sand and mud are bordered with a pempsis (*Pemphis acidula*)-purslane (*Sesuvium portulacastrum*) vegetation, which also surrounds a number of tide pools. Adjacent to the main taxiways near the air terminal is a salt-water pond, a favorite shorebird resting and feeding site, especially at high tide. Along the air strips are more than two miles of grassy vegetation up to 100 feet or more in width on either side. This grassy area is utilized extensively by Golden Plovers and occasionally by Ruddy Turnstones.

Much of the land area of the island is vegetated with an open forest of tree heliotrope (*Tournefortia argentea*). This habitat is utilized by plovers in winter only. Very few shorebirds are found on the eight miles of outer shoreline beaches composed of coralline rubble and reef rock.

MIGRATION

Golden Plovers occur on Wake Island from late summer to late spring, being generally absent from early June to late July. From 8 to 16 June 1963, the only shorebirds observed on the island were a Wandering Tattler (*Heteroscelus incanum*) and a Sharp-tailed Sandpiper (*Erolia acuminata*), each being seen on only one occasion. During the period 20 to 28 July 1963, no shorebirds were present until 27 July when a flock of six plovers, eight turnstones, and one tattler arrived. Alexander Wetmore, who was on Wake in 1923 from 27 July to 5 August, observed 20 or more turnstones, three tattlers, and small flocks of Golden Plovers commonly in southward migration during that period (personal communication). In the period 22 to 30 August 1964 the first plovers were seen on the morning of 28 August, four of them feeding with six turnstones. Between 1200 and 1430 more than 50 additional plovers arrived. These birds left the island during the night or early morning; only four plovers could be found on the following morning. Another flock of 40 or more arrived at midday and once again departed before the next morning, with only eight plovers, five turnstones, and three tattlers present the next day. By 1600 only two plovers and two tattlers remained.

Apparently the first southbound plovers reach Wake Island in late July. These birds do not necessarily arrive in large flocks and seldom remain on the island for more than a few hours. Those individuals that winter on the island evidently arrive at a later date. Unfortunately no observations have been made during peak migration in the fall.

Observations of wintering birds were made from 21 December 1963 to 5 January 1964, and 19 December 1964 to 9 January 1965. In 1963 and 1964 more than 500 plovers were present on the island, but there were only about 200 in 1964 and 1965. Other species were present only in small numbers. Wintering shorebird populations were unstable, with a continuous flux of individuals and small flocks. Adverse weather frequently accompanied the arrival of uncommon species such as Dunlin (*Erolia alpina*), Sanderling (*Crocethia alba*), Greater Yellowlegs (*Totanus melanoleucus*), Snipe (*Capella gallinago*), Pintail (*Anas acuta*), Garganey's Teal (*A. garganey*), and Shoveler (*Spatula clypeata*). These arrivals were sometimes accompanied by new plovers, turnstones, tattlers, and sharp-tails; they seldom remained very long and might represent inter-island movements of many wintering species.

Our earliest spring observations began on 11 April 1964, and at that time less than one-half the number of plovers were present than had been on the island in January. Plover counts were made several times a day until 26 April and indicated a constant flux of birds. Numbers of plovers present on a given day fluctuated from less than 30 to several hundred. Small groups were continually arriving and departing, and the number of birds occupying winter territories steadily decreased during this period.

The period from 8 to 23 May 1965 presented a drastically changed situation. On 10 May only five plovers, six turnstones, and 12 tattlers were present. On 12 May about 25 turnstones and 15 tattlers could be found but only one plover. Five plovers were observed on 13 May, but the number of tattlers and turnstones remained constant. Nearly all individuals of these three species left within the next day or two, and only a few tattlers and turnstones remained on 23 May. Similarly, Bailey (1951) recorded Golden Plovers on Wake between 11 and 15 May in 1949.

On two occasions migrating flocks of plovers were observed leaving the island in the spring of 1964. A quotation from the field notes of Johnston for 18 April is as follows: "I noticed at 3 p.m. $\frac{1}{4}$ mile away a flock of 16 *Golden Plovers* rise from the sand flats and fly straight out of sight over the NNW corner of the lagoon. They did not circle but simply gained altitude straightway and disappeared from my view." For 21 April: "About 4 p.m. we were watching birds over the sand flats at the lagoon. At 4:30 we saw about 9 *Golden Plovers* rise from the flats and, as they gained altitude, the flock was joined by about 15 others. These, then, began to circle, picked up some other plovers until the flock numbered about 30. We were looking directly westward. The birds continued to wheel and circle higher and higher above the lagoon. I watched them for about 5 minutes until they were out of sight. They were probably a mile high . . ."

BEHAVIOR

Behavior of the Golden Plover varied seasonally. Wintering individuals dispersed over the island and occupied almost all available habitats. Territories were established and vigorously defended. The birds became solitary, and rarely were more than two seen together. They paid little attention to nearby aircraft or

vehicles. Evidently new arrivals on the island remained in small flocks, were wary, and did not tolerate a close approach. On several occasions in the spring individuals in flocks, known to be recent arrivals, were found squatting on sandbars, runways, or asphalt water-catchment basins. At no other time were plovers seen squatting. Although this behavior might indicate extreme fatigue following a long-distance flight, the majority of birds in any particular flock were standing.

Territorial behavior diminished during April and was absent among the plovers in May. At this time, however, Wandering Tattlers defended territories even against plovers. At no other season did tattlers exhibit territorial behavior.

MOLT

Henshaw (1910:257), from his observations in the Hawaiian Islands, stated that Golden Plovers in the fall migrate before they molt, and in the spring they molt before they migrate. Our observations, summarized in table 1, do not agree with those of Henshaw. Most of the plovers arriving on Wake Island from the north in August were undergoing body molt, and many had replaced at least one-half of their primaries. No doubt these individuals initiated molt before their departure from the Arctic. Sauer (1962), in fact, detected molt in Golden Plovers on St. Lawrence Island before their southward migration. Conversely, in the spring the plovers on Wake were molting body feathers even until their departure in late April, but many of the premigrants (especially the females) had only partially acquired the breeding plumage. We agree with Henshaw in part, for our fattest males—those which we believed were incipient migrants—were in the most nearly complete breeding plumage. The April females, on the other hand, never reached full breeding plumage on Wake, and therefore must have completed their molt after their arrival in the Arctic.

TABLE 1
SUMMARY OF DATA ON PLUMAGE AND MOLT

Males	Females
April (16 ♂♂, 11 ♀♀)	
All 16 molting body feathers, some sparsely but most in heavy molt.	All 11 molting body feathers, most in heavy molt.
Plumage varied from full breeding type (most birds) to only one in winter plumage.	None in full breeding plumage, rather $\frac{1}{4}$ – $\frac{1}{2}$ of breeding plumage.
August (8 ♂♂, 3 ♀♀)	
Body molt nearly completed in five birds; 1–3 outer primaries still unmolted.	Two not molting—all feathers old and worn.
Three birds not molting but in about $\frac{1}{2}$ winter plumage.	One molting primaries and in about $\frac{1}{2}$ winter plumage.
December (9 ♂♂, 3 ♀♀)	
Sparse body molt in all birds; some still molting primaries and a few molting retrices.	Sparse body molt in all birds; some primary and rectrix molt.
All in winter plumage.	All in winter plumage.

As for molting retrices, our April birds fell into one of two groups. Some individuals had all new retrices, whereas others had replaced all the retrices except

the outer two pairs. By examining molting rectrices in numerous birds, we became proficient in distinguishing new feathers from old ones; the lateral "notches" and tips of the new feathers were distinctly yellower than those same areas (pale white) on the old feathers. Molting rectrices were detected in only three of the August birds but were found in nine birds of the December sample. Rectrix molt begins with the central pair, but from that point laterad the pairs of rectrices are not dropped consecutively. In one August male, for example, pairs (numbered from inside outward) 1 and 2 were new, 3 ensheathed, 4 and 5 old, and 6 ensheathed. Another August male had pairs 4, 5, and 6 all ensheathed, but 6 was longer than 4, which was longer than 5. Some of these variations in the sequence of rectrix replacement may account for variations in color and markings of the outermost rectrices, as discussed below.

SEX AND AGE CHARACTERISTICS

Inasmuch as we were able to net and band a few Golden Plovers, reliable criteria were desirable for the separation of the sexes and age groups in the hand. Some authors contend that Golden Plovers in breeding plumage are alike in color (Ridgway, 1919); others (Witherby *et al.*, 1947; Gabrielson and Lincoln, 1959) suggest minor sexual color differences, the female being browner below and having more white abdominal feathers than the male. The many individuals that we examined in breeding and near breeding plumages showed that the sexes are usually separable in this plumage because the superciliary stripe is usually whiter in the male. This separation, however, may be difficult unless the two extremes are at hand. Another valuable sex characteristic is the color and pattern of the outermost rectrix; in males this feather is usually barred black and white, whereas in females it is virtually unbarred and gray-brown. There is considerable individual variation in these patterns, however; in a few males (proven by dissection) the outer rectrices were unbarred and gray-brown and some females even had these feathers more or less barred like the usual male pattern. These variations were probably not due to age differences alone because most of them were found in birds in breeding plumage.

In the winter plumage the whiteness of the superciliary stripe was unreliable for separating sexes. In our December sample, and in a few April individuals, the only external clues to sex were patterns in the outermost rectrix.

Wing length was unreliable in the separation of sexes (table 2). In wing length our sample from Wake Island, incidentally, resembled more closely the Siberian sample measured by Vaurie (1964).

No satisfactory method for distinguishing first-year birds from adults was found.

TABLE 2
MEAN AND EXTREME WING LENGTHS (IN MM) OF PACIFIC GOLDEN PLOVERS

	N	Males	N	Females
Ridgway, 1919:89 ^a	23	165.9 (147-181.5)	11	167.2 (156-187.5)
Vaurie, 1964:16 ^b				
Siberia	17	165.3 (156-174)	15	165.8 (160-173)
Alaska	30	169.5 (164-177)	16	171.6 (164-180)
Wake Island ^a	28	163.2 (152-171)	15	163.5 (159-168)

^a Chord measurements.

^b Flattened wing.

Certainly our August sample consisted of adults alone because all of them had some black underparts and several were molting primaries and retrices. Upon dissection, no bursa of Fabricius could be located in any of our birds.

BODY WEIGHT AND LIPID VARIATIONS

Twenty-seven birds were weighed in April, 11 in August, and 12 in December (table 3). The April birds, averaging 153 g, were significantly heavier than both the August (133 g; $P < 0.01$) and December (130 g; $P < 0.001$) birds. The birds in April were taken over a wider span of time (16 days) than the August and December samples, however, and probably included both premigrants and intramigrants. The April weight data were definitely bimodal, as is reflected in the frequency distribution of body lipids (fig. 1). The bimodality was not associated with day of the month or sex. There was a conspicuous breaking point in the weights at about 150 g, and not uncommonly our sampling on a given day would yield both heavy (> 150 g) and light (< 150 g) birds. Because increases in body weight can be positively correlated with increase in body lipids (see discussion beyond and fig. 2), it appears likely that the heaviest birds in April were winter residents that had essentially completed premigratory lipid deposition and were ready to migrate.

Baker (1948:133) presented some body weights of Golden Plovers from Guam

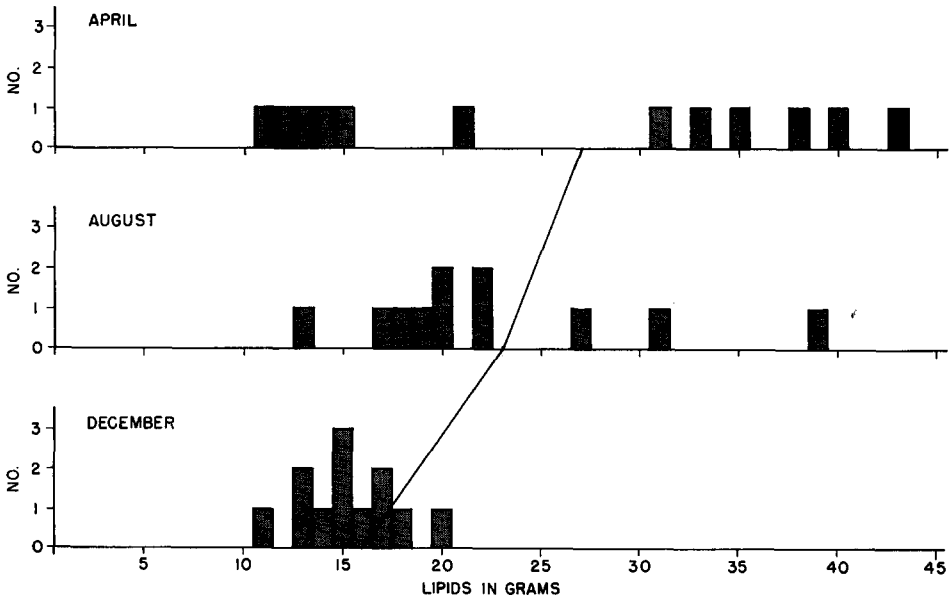


Figure 1. Frequency distribution of total lipids extracted from Golden Plovers. The line descending to the left joins the monthly mean values. Note the bimodal distribution in the April and August samples.

evidently taken in September or October. The averages reported by him (117 g for 7 males and 114 g for 4 females) are conspicuously lower than those from Wake Island in August, but the two samples are probably not comparable because of the different months when collected. His weights (minima of 107 and 109 g) from Guam are among the lightest that are known for this species (cf. table 3). Max Thompson

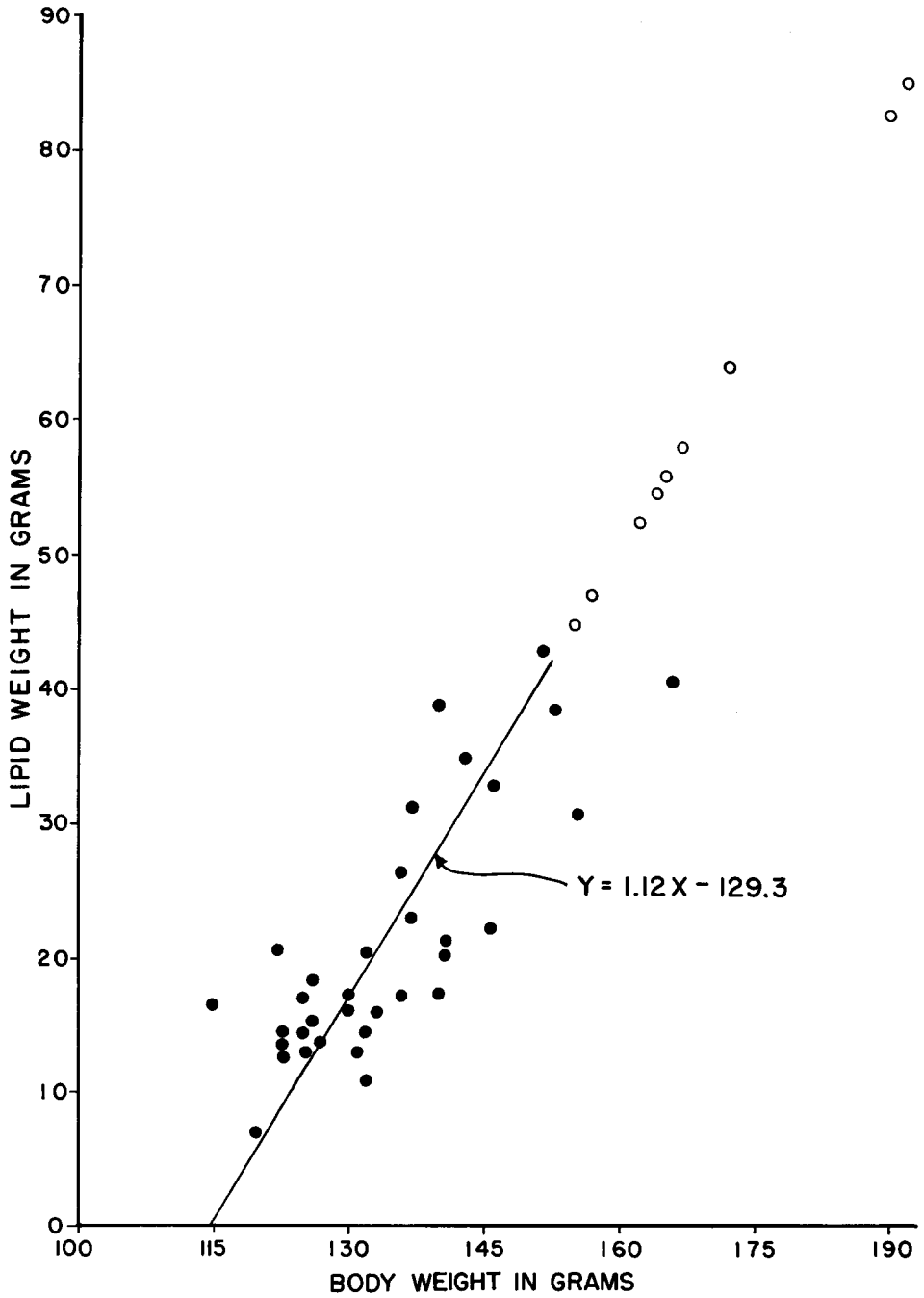


Figure 2. Relationship of body weight and total lipids extracted from Golden Plovers. Blackened circles = empirical data; open circles = estimates of total lipids in birds of known body weight, based on the least-squares regression equation.

TABLE 3
WING LENGTHS, WEIGHTS, AND EXTRACTED COMPONENTS OF PACIFIC GOLDEN PLOVERS

	Wing length, mm ^a		Body weight, g		Water, g		Nonlipid dry, g		Lipid, g	
	N	Mean ± sd	N	Mean ± sd	N	Mean ± sd	N	Mean ± sd	N	Mean ± sd
April										
Males	16	165.0 ± 1.6 (156.0–171.0) ^b	16	151.5 ± 18.9 (121.9–192.1)	7	67.8 ± 3.8 (62.9–72.0)	7	44.9 ± 5.2 (37.4–53.5)	7	26.9 ± 11.8 (11.2–43.2)
Females	11	163.2 ± 2.5 (159.0–166.0)	11	154.2 ± 16.7 (122.5–172.3)	4	68.2 ± 4.0 (63.5–72.8)	4	47.2 ± 5.6 (39.7–53.2)	4	26.4 ± 14.9 (14.5–40.3)
August										
Males	4	158.8 ± 7.4 (152.0–169.0)	8	132.9 ± 10.1 (115.0–145.8)	8	72.1 ± 7.9 (61.5–82.4)	8	37.8 ± 4.2 (31.0–43.4)	8	23.0 ± 8.1 (13.4–38.7)
Females	2	166.0 (164.0–168.0)	3	133.2 (125.8–137.6)	3	73.3 (68.4–77.1)	3	37.7 (34.1–41.2)	3	22.2 (17.2–26.7)
December										
Males	8	161.9 ± 4.2 (158.0–167.0)	9	131.5 ± 6.9 (120.7–141.0)	9	76.5 ± 2.4 (73.8–80.1)	9	39.9 ± 3.4 (37.2–46.5)	9	15.1 ± 3.1 (7.4–20.8)
Females	2	163.0 (162.0–164.0)	3	127.5 (123.2–133.2)	3	75.4 (73.6–78.9)	3	37.0 (35.0–38.4)	3	15.1 (14.4–15.9)

^a Chord.

^b Numerals in parentheses indicate range of values.

has kindly supplied us with some unpublished weights of Golden Plovers from the Pribilof Islands, taken between 6 August and 7 September. The weights, probably not premigratory maxima in all instances, ranged between 131.1 and 251.5 g, averaging 174.5 g for 21 adults. Four of these adults exceeded our Wake Island birds in weight: 208.6, 212.5, 213.5, and 251.5 g.

The results of the carcass analysis from the Wake Island samples are summarized in table 3. Of particular importance are the seasonal differences in body lipids: average body lipids in April and August, although not significantly different from each other, are both significantly greater ($P < 0.05$) than in the December sample. As with body weights, lipids from the April birds are bimodally distributed (fig. 1), and the bimodality could not be associated with sex or day of the month. Even though the August sample was obtained in only two days, there is also a trend toward bimodal distribution of the lipid values. In this case, however, the leaner birds were taken on 28 August and the fatter birds (from a different flock) on 29 August.

Some of the carcass components of the heaviest birds of the April sample were accidentally lost during analysis. On the basis of the reasonable assumption that the relationship between body weight and lipid weight is essentially linear through the maximum weights included in the samples, it is possible to estimate the lipid contents of the heaviest specimens (fig. 2). These, with body weights of 192.1 g and 190.5 g, contained approximately 85 g and 83 g of lipid, respectively. Thus, fat comprises a maximum of about 44 per cent of live weight, or about 180 per cent of the nonfat dry weight (ca. 46 g) in this sample of Golden Plovers. This compares with mean values of about 49 per cent (live weight) and 300 per cent (nonfat dry weight) found by Odum (1965) in several species of small passerines ready for trans-oceanic flights. A comparison between our data and his suggests that Golden Plovers, and perhaps other long-range migrants of similar body size, cannot deposit

or transport the same relative weight of lipids as can smaller migrant birds. In terms of bioenergetics of flight, it would appear that Golden Plovers compensate for these relatively smaller lipid quantities by having greater flight speeds than small migrant passerines.

RATES OF METABOLISM AND ESTIMATED FLIGHT RANGES

Two male Golden Plovers were captured on Wake Island in December 1964 and were maintained in captivity at the University of Florida until March 1965. At that time basal rates of metabolism were obtained at night by measuring oxygen consumption. One bird, weighing 140 g, evidently never reached a basal level, our minimum value for it being 1.38 cc O₂/g-hr. at 32° C. The other bird, weighing 118 g, attained minimum values of 0.88 and 1.06 cc O₂/g-hr. at 31° C. Using an average of the last two figures, the equivalent BMR is 0.0047 kcal/g-hr. If one uses the King-Farner equation (1961) for basal rates of metabolism in large birds, the predicted values are 1.09 cc O₂/g-hr. or 0.0052 kcal/g-hr. for a bird the size (fat-free weight) of a Golden Plover. Our values, then, fall within the 20 per cent deviations predicted by the King-Farner equation for a bird of this size.

In recent years a variety of methods have been postulated for the estimation of flight energy requirements in birds (see reviews by Nisbet *et al.*, 1963; Dolnik and Blumenthal, 1964). The theoretical calculations advanced by Nisbet *et al.* (1963) and the estimates of Pearson (1964) are not considered here because, in terms of the so-called "weight loss method," we have virtually no quantitative data for the Golden Plover. Rather, it is our conviction that the experiments of LeFebvre (1964), Hart and Roy (1966), and Tucker (1966) have resulted in the best physiological bases to date for determining metabolic requirements in flight. LeFebvre's revelation that flight metabolism is approximately eight times basal rate of metabolism in pigeons is close to the indirect estimates of Dolnik and Blumenthal (1964) for passerines. They reported that flight energy requirements are 3 to 4 times existence energy requirements and that the latter are 1 to 2 times basal requirements.

Cooke (1937:7) gives two flight speeds for the European Golden Plover (*Pluvialis apricaria*) (see also Meinertzhagen, 1921), 60 and 70 mph, and two for the American Golden Plover (*P. d. dominica*), 60 and 70 mph. It seems reasonable to accept an average flight speed of 65 mph for *P. d. fulva*. Sauer (1962), without any substantiating evidence, suggested a speed of only 40 mph. Stresemann (1934) assumed that an average-sized waterbird like a Golden Plover would fly at 26 m/sec. and made two wing beats each second. A flight from the Aleutians to Hawaii, he predicted, would require about 35 hours and 252,000 wing beats. The flight speed would be 58 mph, only a little less than the actual values reported by Cooke (1937) for *P. d. dominica*.

With these various data (flight speed, lipid quantities, and rate of metabolism in flight), it now becomes possible to estimate flight distances in the Golden Plovers obtained on Wake Island. These are summarized in table 4 where, for each of the sampling periods, we have calculated flight estimates for birds of average fat-free weight and for the fattest and leanest individuals. We feel justified in using fat-free weight as the basis for calculating energy requirements in flight because the rate of basal metabolism (from which flight metabolic rate was computed) was obtained from a light individual weighing, on the average, 118 g, a value close to the fat-free

TABLE 4
BODY WEIGHTS AND ESTIMATES OF FLIGHT DISTANCE^a

	Body weight, g	Fat-free weight, g	Fat, g	Hours in flight	Miles
April					
Average (11)	140.5	113.7	26.8	56	3640
Fattest bird	151.5	108.3	43.2	96	6260
Leanest bird	122.5	109.7	12.8	28	1830
August					
Average (11)	133.0	110.2	22.8	50	3250
Fattest bird	140.7	102.0	38.7	92	5980
Leanest bird	125.2	111.8	13.4	29	1890
December					
Average (12)	130.5	115.4	15.1	32	2060
Fattest bird	129.9	112.0	17.9	39	2510
Leanest bird	120.7	113.3	7.4	16	1030

^a Assuming that average flight speed = 65 mph, that flight-energy expenditure = $8 \times$ basal rate of metabolism, and that the caloric density of fat = 9.1 kcal/g (Johnston, unpublished data).

weight in this species. It should be evident that our flight estimates are probably maximum values and do not take into account variables such as head or tail winds.

Reconsideration of the weight and lipid data from the April and August samples permits another observation and prediction. Assuming flight metabolism to be $8 \times$ BMR, a plover with a fat-free weight of 113 g (average for April birds) would need 18 g fat to be able to fly nonstop from Wake Island to the Aleutians or Kamchatka Peninsula, a distance of 2400 miles. The flying time would normally be 37 hours, and the minimum body weight at the start would be 131 g. Our data in August, however, showed that five plovers just arriving on Wake Island from the north had an average body weight of 125 g, an average fat-free weight of 107 g, and 18 g of fat. If 18 g of fat are required for the average plover to span the Wake-northward distance, then the minimum premigratory body weight of 131 g predicted above is too low and should be approximately 143 g. Interestingly enough, as pointed out above, body weights of our April sample were bimodal with the dividing point being about 150 g. We speculate, therefore, that only Golden Plovers weighing at least 150 g attempt this 2400-mile flight.

Lincoln's account (1950:70) of an American Golden Plover migrating nonstop from Nova Scotia to South America has been widely cited as a classic example of long-distance migration in birds. Closer examination of his account, however, reveals several unfounded statements and estimates that now require correction. The basis for his account was a bird banded in Quebec on 5 September 1948 and recovered in British Guiana on 30 January 1949. Lincoln assumed that this bird took off from Nova Scotia and flew "the entire distance of 2,400 miles . . . to South America without stop, probably requiring about 48 hours of continuous flight." Although his assumption may be true, it is certainly possible that this bird could have followed the coastline of the eastern United States even as far south as Florida before attempting an overwater flight. Indeed, there are numerous records for this species in autumn along the Atlantic coast (see, for example, Urner, 1929). Furthermore, the bird could have landed in the West Indies (Bond, 1961) or Trinidad (Herklots, 1961), where there are also numerous records, before proceeding to British Guiana.

The point is, one cannot be certain that this bird flew nonstop "from Nova Scotia to South America." There might be a major flight of Golden Plovers over the western Atlantic Ocean as Lincoln depicts (1939, fig. 12) and Tufts (1961) suggests, but if that were true one would expect to find concentrations of plovers in autumn in Labrador or Newfoundland. Both Austin (1932) and Peters and Burleigh (1951) recorded this species as uncommon or casual in autumn. We favor the ideas expressed by both Austin (1932) and Tufts (1961) that some Golden Plovers may take the shortest route possible (overwater), but others travel along the Atlantic coast to more southern points before undertaking a strenuous flight. Certainly, we disagree with Sprunt's implication (1954) that all "the birds which appear at South Atlantic localities have been forced in by abnormal conditions."

Finally, our present knowledge of flight speed in this species supports a flying time of 37 hours (not 48) for a distance of 2400 miles. Lincoln went on to suggest that this flight was "accomplished with the consumption of less than 2 ounces [56 g] of fuel in the form of body fat." It is probable that Lincoln got this idea from Cooke (1915:35) who stated that "... less than 2 ounces of fuel in the shape of body fat suffice to force the bird at a high rate of speed over that 2,400-mile course." No evidence was presented that any plover was ever weighed, but from our data on the migrating Pacific Golden Plovers, it would appear that Lincoln's bird (if it did fly 2400 miles nonstop) probably lost only about 18 g of fat, one-third of the amount that he proposed.

SUMMARY

Movements, population fluctuations, and other migratory aspects of the Pacific Golden Plover were observed on Wake Island periodically between June 1963 and May 1965. Optimal habitat for plovers on the island included grassy areas beside the air strips and the sand and mudflats bordering a large lagoon. Northbound migrants became especially conspicuous in late April, and southbound migrants evidently began arriving on the island in late July or August. A significant number of the plovers overwinter on Wake Island where they establish territories; yet during the autumn and spring daily variations in numbers indicated much inter-island movement.

Periodically, samples of plovers were collected for studies of molt, body weight, and lipid extractions. In 1964 27 birds were taken in April, 11 in August, and 12 in December. An additional two birds were taken alive in a mist net for measurement of basal rate of metabolism. Both the April and August migrants were molting body feathers; molting primaries were detected in August (and a few December) birds. Thus, our data do not confirm the contention of Henshaw that Golden Plovers in the spring molt before they migrate or, in the autumn, migrate before they molt. Among the December birds sparse body molt was noted, but some were still molting primaries and rectrices.

On the average the April birds weighed more (153 g) than the August (133 g) and December birds (130 g). Maximum weights in April were 192.1 and 190.5 g. Despite these average body weight differences, the average body lipids in April and August were similar (26.5 and 22.8, respectively). Lipid contents amounted to a maximum of 180 per cent of the nonfat dry weight, a value which is considerably less than that obtained by other workers for small migrating passerines.

Basal rate of metabolism was found to be 0.0047 kcal/g-hr. at 31° C. Flight speed for the species is believed to be about 65 mph, and we assume, from the

investigations of LeFebvre, that flight energy expenditure is eight times the basal rate. Thus the fattest (by extraction) plovers in April had an estimated flight range of about 6200 miles; those in August, 5900 miles; and those in December, 2500 miles. Our combined data also indicated that only a plover containing at least 18 g of lipids and weighing about 150 g will attempt the 2400-mile flight from Wake Island to the Aleutian Islands or Kamchatka Peninsula, or vice versa. Plovers arriving on Wake in the autumn from the north still contained, on the average, 22 g of lipids.

Details of migration in the American race of the Golden Plover are also discussed and re-examined. We believe, contrary to earlier estimates, that if these birds do fly nonstop from Nova Scotia to South America, they accomplish the flight in some 37 hours and consume only about 18 g of lipids.

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