FAT CYCLICITY, PREDICTED MIGRATORY FLIGHT RANGES, AND FEATURES OF WINTERING BEHAVIOR IN PACIFIC GOLDEN-PLOVERS[1]

OSCAR W. JOHNSON

Department of Biology, Moorhead State University, Moorhead, MN 56560

MARTIN L. MORTON

Department of Biology, Occidental College, Los Angeles, CA 90041

PHILLIP L. BRUNER

Department of Biology, Brigham Young University–Hawaii, Laie, HI 96762

PATRICIA M. JOHNSON

Department of Biology, Moorhead State University, Moorhead, MN 56560

Abstract. Annual cyclicity of body components in wintering Pacific Golden-Plovers (*Pluvialis fulva*), combined with ecological and behavioral features were variously studied from 1978 through 1987. The primary research site was in Hawaii at the Bellows Air Force Station (BAFS), Oahu. After fall arrival, body weights trended downward for several weeks, possibly in response to the energy required for the behaviors associated with establishing (and reestablishing) residency combined with molting. Major premigratory weight gains began in late March about 1 month prior to migration. Statistical correlations between body weight and fat content are described. Premigratory dehydration as an adaptation to increase flight range and/or energy stores at the migratory destination was likely.

Fat-free dry weights (FFDW) at BAFS were least in the fall and greatest in the spring. For juveniles, this difference relates to overall body growth during the first wintering season. With older birds, it may reflect the environmental conditions at the respective end points of migration—predictably favorable for southbound migrants, unpredictable for northbound birds. Plovers wintering on Enewetak Atoll and Wake Island had significantly higher FFDWs than the birds at BAFS. Possible factors in this relationship are discussed.

The BAFS population contained many territorial birds, and showed high rates of survival and site fidelity over successive years. Juveniles arriving on the wintering grounds for the first time probably experience considerable mortality as they compete with established adults for space and resources. Based on wing lengths, many of the plovers involved in this study were from Alaska breeding grounds. Flyways to the tundra may involve staging areas, but specific information is lacking. Using current formulae, we describe the relationship between body weight and flight range, and provide estimates of the fat required to reach various landfalls.

Key words: Pacific Golden-Plover; Pluvialis fulva; fat cycle; wintering behavior; migration; flight ranges.

INTRODUCTION

Many shorebirds perform lengthy migrations between summer and winter ranges often involving nonstop transoceanic flights. The fat cycle associated with these remarkable abilities, and also the relationship between fat stores and winter survival have stimulated considerable interest in recent years. Much has been learned about wintering shorebirds particularly in the Old World (Davidson 1981, Pienkowski and Evans 1984,

Pienkowski et al. 1984, Piersma et al. 1987). Comparable studies in the New World have produced significant advances (Senner and Howe 1984, Morrison and Myers 1987), but major gaps in knowledge remain. Relatively little is known about the insular wintering grounds of the tropical Pacific. These areas are occupied even during the summer months as young shorebirds often do not return north in their first spring, and are used intensively by adults and young alike through the wintering season. Pacific shorebirds are of fundamental importance in tropical ecosystems, yet with only a few exceptions, the ecol-

ogy, behavior, and migratory pathways of these birds are poorly understood (Thompson 1973, McClure 1974, Johnson 1979, Morrison 1984, Pienkowski and Evans 1984, Parish et al. 1987).

We follow various authors and organizations (British Ornithologists' Union, Ornithological Society of New Zealand) in regarding the Pacific Golden-Plover, *Pluvialis fulva*, as a separate species from the American Golden-Plover, *P. dominica* (Kinsky and Yaldwyn 1981, Connors 1983, Gochfeld et al. 1984, Hayman et al. 1986, Knox 1987, Lane 1987). (See AOU 1983 for the subspecies alternative.) *Pluvialis fulva* breeds from the Yamal Peninsula in Siberia eastward to western Alaska, and winters throughout Oceania and along coastal Asia (AOU 1983). It is a conspicuous member of the Pacific avifauna, and among the world's foremost long-distance migrants. Based on the occurrence of certain North American shorebirds in Hawaii (Bristle-thighed Curlew, *Numenius tahitiensis,* and Wandering Tattler, *Heteroscelus incanus*) and an absence of Eurasian forms, Henshaw (1910) postulated that Pacific Golden-Plovers wintering in Hawaii breed in western Alaska. A broader concept, the "Nearctic-Hawaiian Flyway," the northern end of which extends from western Canada to northeastern Asia was put forth by Baker (1951). Extensive banding studies of Ruddy Turnstones, *Arenaria interpres* (Thompson 1973, McClure 1974), and shorebird occurrence records through the years (concisely summarized by Pratt et al. 1987) substantiate Baker's proposed corridor. Since 1958, about 900 *P. fulva* have been banded on Pacific wintering areas (mostly in the Hawaiian Islands, some at Johnston Island and various of the Marshall and Line islands); and nearly 300 in the Pribilof Islands (these were captured during fall migrations from 1964–1968 and probably were birds enroute from northeastern Siberia, this is the only significant banding effort for *P. fulva* in Alaska). Unfortunately, there have been no band returns which shed any light whatever on the locations of breeding grounds for plovers wintering in Hawaii and elsewhere in the central Pacific. Pending such definitive records, it is reasonable to assume that Hawaii birds are not necessarily restricted to the western Alaska portion of the breeding grounds and may range to northeastern Siberia. From Hawaii's geographic location in the flyway, direct north–south flights are likely.

In this paper, we describe total weight, fat content, and other body parameters of plovers from the time of their fall arrival on a winter range in Hawaii until their departure the next spring. We also include data from plovers wintering on Enewetak Atoll, northwest Marshall Islands. The latter findings allow comparisons between two widely separated Pacific wintering grounds, and complement a previous investigation dealing with the fat stores of plovers oversummering on Enewetak (Johnson and Morton 1976). Where possible, we will relate fat cyclicity and body components to other aspects of wintering biology including behavior and molt, and to the earlier studies of Johnston and McFarlane (1967).

METHODS

The specimens from Hawaii ($n = 81$, 60 adults and 21 juveniles) were collected during the wintering season of 1979–1980. Sampling began on 17 August 1979, and continued at intervals through 27 April 1980 when the birds departed on northward migration. The collection site was Bellows Air Force Station (BAFS) located near the town of Waimanalo on the east coast of Oahu (approximately 21°N, 158°W). BAFS is an inactive military reservation of about 600 ha containing an abundance of plover habitats such as lawns, pastures, and unused runways (Johnson et al. 1981). About 300 plovers winter at BAFS; these birds have been under continuous study since 1979 by Johnson, Bruner, and Johnson. The Enewetak Atoll specimens ($n = 52$, 25 adults and 27 juveniles) were collected by O. Johnson and M. Morton over the period 22–26 November 1978. At that time, Enewetak (approximately 11°N, 162°E) held a substantial population of wintering plovers with at least 250 birds seen during partial surveys of the atoll. All of the collected birds (BAFS and Enewetak specimens) were used in earlier work on plumages and molts (Johnson and Johnson 1983).

Each specimen was weighed (to the nearest gram with a Pesola scale) immediately upon collection. Thereafter, an entire wing (usually the right) and the rectrices were removed and saved for studies of molt, reproductive tissue samples were excised, and age (adult or juvenile) determined through plumage characteristics and condition of the cloacal bursa. Each retained wing was weighed and measured (flattened chord from carpal joint to tip of longest primary, as described by Prater et al. 1977) when removed, then oven-dried and reweighed. The resultant figures were

TABLE 1.   Total weights and body components in adult Pacific Golden-Plovers collected on winter ranges in Hawaii and Enewetak Atoll.

	Fall Arrival period 17 Aug–13 Sept 1979[a] Hawaii n = 17			Early Winter 22–26 November 1978[b] Enewetak n = 25		
	$\bar{x}$	(Range)	SE	$\bar{x}$	(Range)	SE
Total weight[d]	117.5	(102–138)	2.0	118.3	(100–148)	2.5
Total fat	9.9	(3.3–27.0)	1.5	13.3	(5.5–32.4)	1.5
Fat-free weight	107.6	(93.0–120.4)	1.8	105.0	(93.7–120.6)	1.4
Weight of water	72.4	(59.3–81.1)	1.5	64.9	(56.6–71.9)	0.7
Total dry weight	45.1	(37.5–60.6)	1.6	53.5	(41.8–77.4)	2.2
Fat-free dry weight	35.2	(31.7–42.3)	0.7	40.1	(31.5–50.4)	0.9
Fat, % of total weight	8.3	(3.0–22.5)	1.2	10.8	(5.1–22.2)	0.9
Fat, % of total dry weight	20.7	(8.2–44.6)	2.3	23.6	(12.7–42.0)	1.6
Water, % of total weight	61.7	(49.4–66.5)	1.0	55.2	(44.1–61.0)	0.9
Water, % of fat free weight	67.2	(62.9–71.3)	0.5	61.8	(55.7–66.6)	0.5
Liver, total weight[c]	2.7	(1.5–3.8)	0.2	3.4	(1.9–4.5)	0.1
Liver, % fat of dry weight	10.9	(7.3–22.7)	0.9	7.0	(2.3–23.8)	1.0

[a] All dates shown in the table represent the time spans over which specimens were collected. We sampled fall adults opportunistically, making no effort to be selective. Nevertheless, the resultant sex ratio was skewed toward females (14:3) suggesting that females precede males in southward migration.
[b] Early winter sampling was restricted to Enewetak, no comparable Hawaii birds were collected.

added to values for the remainder of the carcass, thus measurements of total dry weight and total weight of water include the retained wing. The term "juvenile" as used here refers to approximately the first 10 months of life, and is applied to the individual from arrival on the wintering grounds in the fall of one calendar year until the spring of the following calendar year. At that time, the young bird either migrates or stays on the wintering grounds and oversummers. Oversummering birds remain lean and often fail to develop breeding coloration. Absence of primary molt in juveniles (it is deferred until the second wintering season at which time the juvenile primaries are very worn) is a useful age criterion. Detailed information on plumages, molts, and age determination is provided by Johnson and Johnson (1983).

Carcasses (less one wing) were preserved in a 4% aqueous solution of formaldehyde and sent to Morton's laboratory for extraction of lipids. Livers were excised from their carcasses and their lipid contents analyzed separately. By excluding one wing from lipid extraction, we introduced a slight error in the measurement of total lipids. However, it is reasonable to assume that the fat lost was negligible in relation to the major fat stores of the body. In the extraction procedure, carcasses and livers were dehydrated in a vacuum oven at 55°C, homogenized, and extracted with petroleum ether in a soxhlet apparatus for 24 hr. Any residual water was taken up with anhydrous sodium sulfate, then the extract was filtered and the ether evaporated.

In addition to the collected specimens, weight and plumage data were obtained from 130 birds captured for banding in mist nets at BAFS. The sample is cumulative and represents total plovers caught in successive wintering seasons from 1979 through 1987. We captured birds over the entire 1979–1980 season, in most other years netting was restricted to the spring. Birds were netted in the semidarkness of the early morning (over about a 45-min period ending with sunrise) as they returned to the study area from overnight roosts on nearby islands. Upon capture, each bird was weighed (to the nearest gram with a Pesola scale), and its right wing measured (flattened chord). The individual's body plumage was evaluated according to a series of stages (Johnson and Johnson 1983) representing degrees of basic and alternate feathering. Primary molt was scored on the right wing using Ashmole's (1962) system wherein 0 = old feather, 1 = a missing feather or one in pin stage, 2–4 = progressive stages of growth, 5 = a fully-grown feather that has lost its sheath. Thus, a total score of 0 indicates worn primaries with no molt underway; from 1–49 represents progressive degrees of molt and feather growth; and 50 indicates 10 new, fully-developed primaries. Since birds were captured before they had begun to forage for the day and experienced stress in the netting procedure, their total weights were at minimal levels.

TABLE 1. Extended.

Mid- to Late Winter 18 Dec 79–19 March 80 Hawaii n = 21			Premigratory period 9–16 April 1980 Hawaii n = 15			Migratory Departure 23–27 April 1980[c] Hawaii n = 7		
x̄	(Range)	SE	x̄	(Range)	SE	x̄	(Range)	SE
130.0	(118–144)	1.4	164.7	(152–178)	1.7	172.1	(152–188)	4.6
14.0	(7.6–24.2)	1.1	39.1	(27.0–47.9)	1.3	55.5	(48.4–68.2)	2.3
115.9	(105.1–124.2)	1.0	125.6	(114.1–135.3)	1.6	116.6	(103.6–127.0)	2.6
78.8	(70.3–87.2)	0.9	84.0	(76.0–92.6)	1.2	77.0	(64.3–84.2)	2.3
51.2	(43.1–63.5)	1.2	80.6	(69.2–89.3)	1.3	95.2	(85.0–107.3)	2.8
37.3	(34.1–41.0)	0.4	41.6	(37.3–48.9)	0.9	39.6	(35.4–44.2)	1.0
10.7	(5.8–17.6)	0.8	23.7	(17.8–29.6)	0.8	32.2	(30.3–36.3)	0.7
26.7	(16.3–39.4)	1.5	48.3	(39.0–55.7)	1.2	58.2	(54.1–63.6)	1.1
60.6	(55.5–64.5)	0.6	51.0	(46.9–54.7)	0.6	44.7	(42.3–47.5)	0.6
67.9	(66.0–70.9)	0.3	66.9	(63.4–70.2)	0.5	65.9	(62.0–68.5)	0.9
3.4	(2.2–4.3)	0.1	4.2	(2.7–6.4)	0.2	4.2	(2.4–5.7)	0.4
14.5	(9.5–23.2)	0.8	26.1	(14.9–49.5)	3.1	36.9	(22.0–48.9)	4.1

[c] Specimens were collected on 23 and 27 April, on 25–26 April approximately 80% of the plovers wintering at BAFS migrated. Since 1980, the pattern has remained remarkably constant with departure typically near the end of April.
[d] All weights in grams.
[e] All body components and calculations above include the liver.

Estimates of flight range involve the interrelationship between fat stores, rate of energy use, and flight speed. The topic has been extensively reviewed by Davidson (1984a) who points out many of the difficulties inherent to these calculations. McNeil (1969), using Raveling and LeFebvre's (1967) formula for flight metabolism (based on passerines and nonpasserines combined), developed an equation for predicting flight range in shorebirds and applied it to a variety of species (McNeil 1970; McNeil and Cadieux 1972a, 1972b). Summers and Waltner (1979) refined McNeil's equation to account for loss of weight during flight. In turn, Davidson (1984a) modified the Summers and Waltner formula by changing the value for flight metabolism to that of nonpasserines (as estimated by the formula of Kendeigh et al. 1977). Recent findings (Castro 1987, Kersten and Piersma 1987) indicate that shorebird basal metabolic rates are higher than previously recognized (i.e., similar to passerines). Pending further studies (particularly of shorebird flight metabolism), we have used both the Davidson, and the Summers and Waltner formulae. They are, respectively: $R = 95.447 \times S \times (T^{0.302} - M^{0.302})$ and $R = 163.24 \times S \times (T^{0.256} - M^{0.256})$, where R = flight range in km, S = flight speed in km/hr, T = total weight in g, and M = fat-free weight in g. The latter formula predicts somewhat longer ranges (by about 16%) than the former. Whenever we give flight-range calculations, the formula used will be identified as: Dav. (Davidson) or S&W (Summers and Waltner).

Statistical analyses included independent sample t-tests, regression analysis, and correlation analysis (Snedecor and Cochran 1980). Results of two-tailed significance tests are reported throughout.

RESULTS

PRELIMINARY COMMENTS

From collected birds, we determined body composition and various associated parameters; the netted birds furnished information on weight and external features only. Each of the two sample groups was divided into consecutive periods reflecting the chronology of events that comprise the wintering cycle (Tables 1, 2; Fig. 1). Since no birds were collected near the end of March, the Early Spring period (Fig. 1) does not appear in Tables 1 and 2; conversely, we elected not to capture birds in late April (as we were concerned about stressing them just before migration), thus the Migratory Departure period does not appear in Figure 1. We made an extensive series of comparisons involving total weights and wing lengths as general indicators of body size and proportions. Tests among and between collected and netted birds showed no significant differences attributable to sexual dimorphism (Connors 1983 reported similar findings), age, or location (i.e., the BAFS samples compared to the Enewetak samples). Therefore, most data were pooled. It was useful to separate the two age groups when analyzing body components (Tables 1 and 2), in
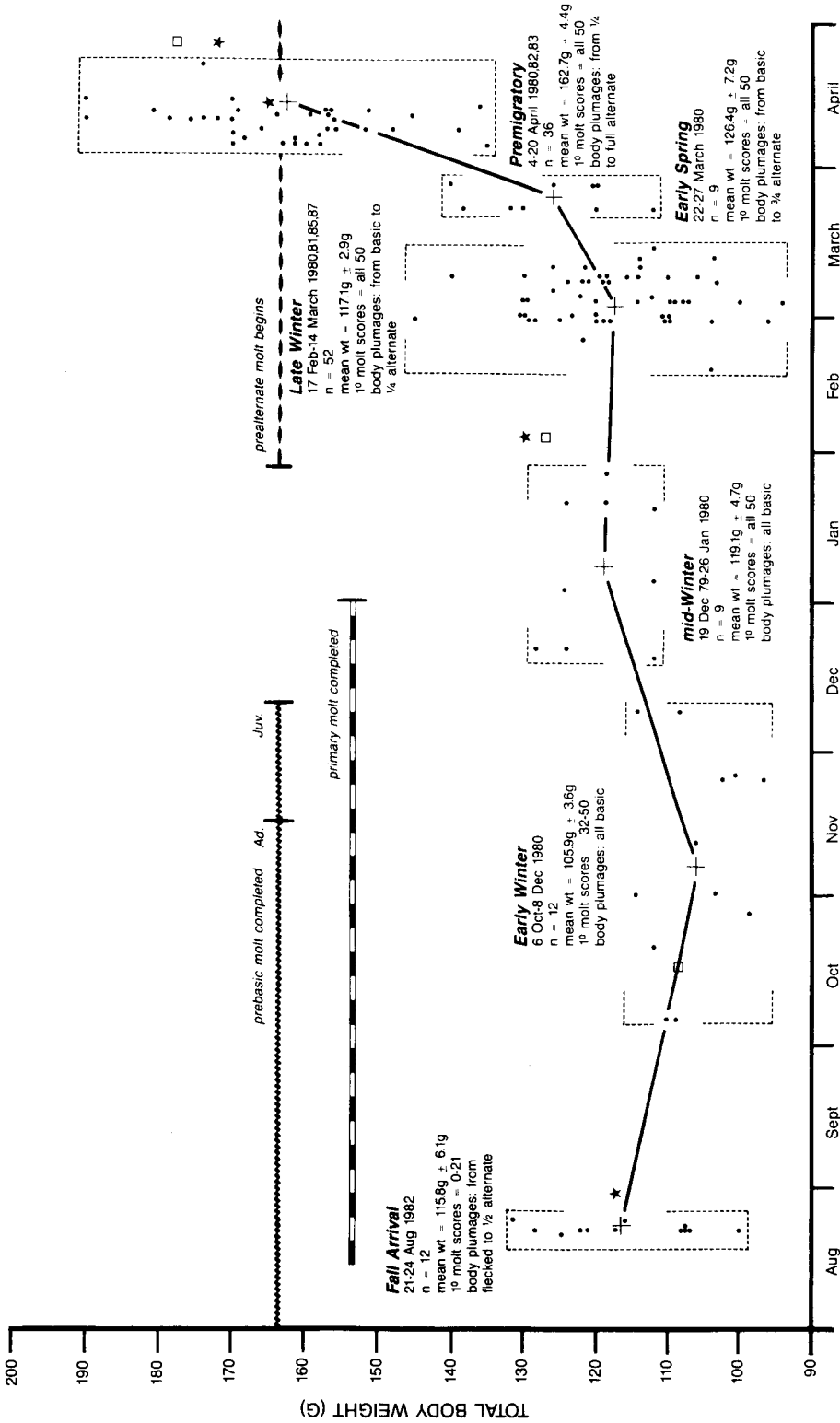
FIGURE 1.   The seasonal body weight cycle of Pacific Golden-Plovers captured for banding at BAFS shown in relation to cycles of molt. Horizontal lines denoting molt indicate the time span over which feather loss and replacement occurs. The + symbol represents the mean for each sample group. The fall sample consists of adults only, other samples are pooled adults and juveniles with adults predominating about 3:1. Captions include: sample size, mean, 95% confidence limits of the mean, and information concerning molt. Features of the latter are explained in the text. Means for sample groups of collected birds are also shown: blackened stars = adults, open squares = juveniles.
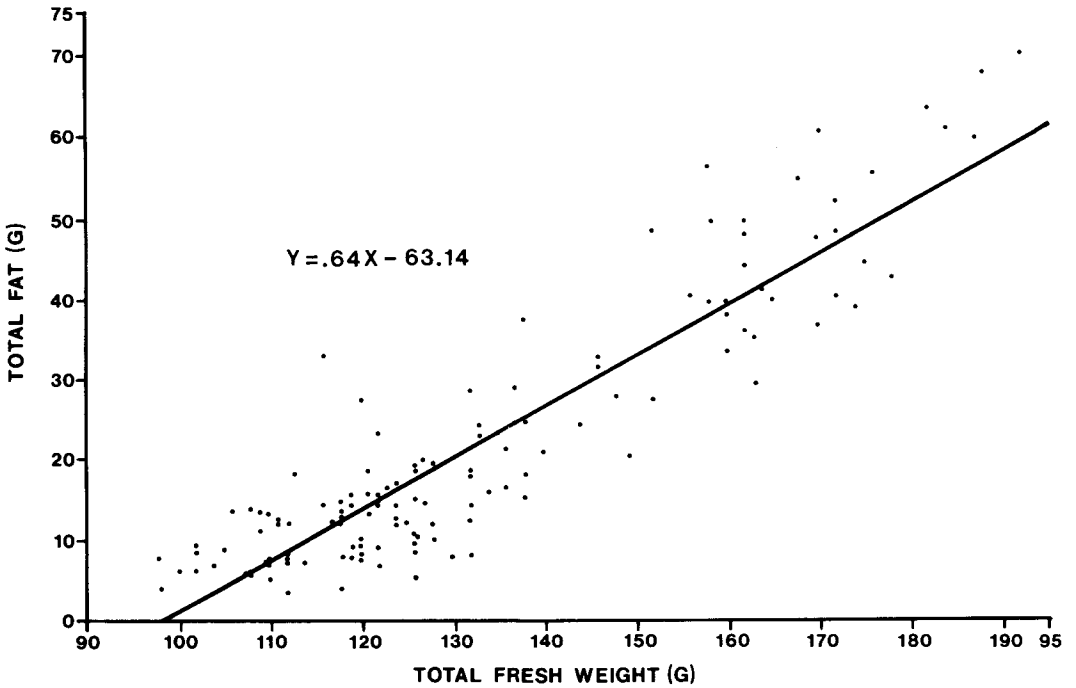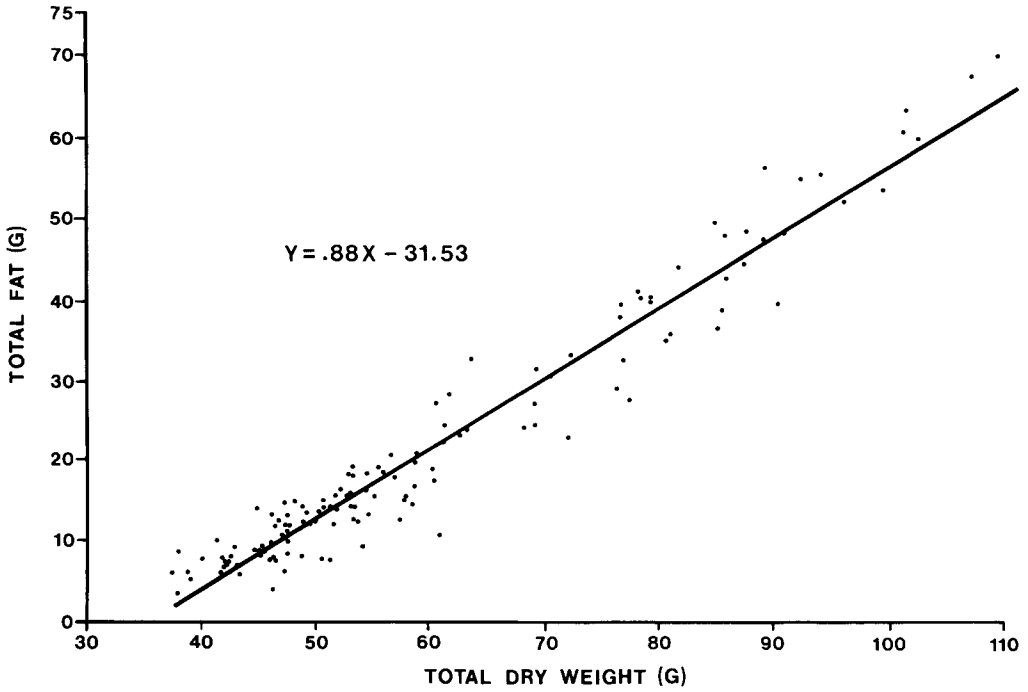
FIGURE 2.   Total fresh weight and total dry weight as related to fat content in Pacific Golden-Plovers wintering at BAFS and Enewetak, $n = 133$.

TABLE 2.   Total weights and body components in juvenile Pacific Golden-Plovers collected on winter ranges in Hawaii and Enewetak Atoll.

	Fall Arrival period 3–28 October 1979[a] Hawaii n = 4			Early Winter 22–26 November 1978[b] Enewetak n = 27		
	$\bar{x}$	(Range)	SE	$\bar{x}$	(Range)	SE
Total weight[c]	108.5	(94–126)	6.5	120.4	(102–160)	2.3
Total fat	16.9	(7.7–32.4)	5.0	15.6	(6.0–39.4)	1.3
Fat-free weight	91.6	(83.6–107.1)	4.6	104.8	(92.6–120.6)	1.3
Weight of water	59.6	(52.3–72.6)	3.9	64.4	(55.7–71.8)	0.8
Total dry weight	48.9	(38.2–63.7)	5.2	55.9	(45.2–90.6)	1.8
Fat-free dry weight	32.0	(29.7–34.5)	0.9	40.3	(34.6–51.2)	0.8
Fat, % of total weight	14.9	(7.9–27.9)	4.0	12.6	(5.6–24.6)	0.8
Fat, % of total dry weight	31.9	(19.2–50.9)	6.3	27.0	(12.7–43.5)	1.3
Water, % of total weight	55.3	(45.0–59.4)	3.0	53.8	(43.4–58.2)	0.7
Water, % of fat-free weight	64.9	(62.5–67.8)	1.0	61.5	(56.0–66.2)	0.5
Liver, total weight[f]	2.0	(1.6–2.6)	0.2	3.6	(2.7–5.4)	0.1
Liver, % fat of dry weight	11.7	(5.4–16.5)	2.1	6.0	(2.0–16.7)	0.6

[a] All dates shown in the table represent the time spans over which specimens were collected.
[b] Early winter sampling was restricted to Enewetak, no comparable Hawaii birds were collected.
[c] This sample was complicated by the individual variation associated with oversummering behavior (see text).
[d] Specimens were collected on 23 and 27 April, on 25–26 April approximately 80% of the plovers wintering at BAFS migrated. Since 1980, the

other considerations (Figs. 1 and 2, and regression analyses of liver lipids) adults and juveniles were combined.

There was no significant difference ($P = 0.118$) between the wing lengths of birds collected at BAFS and Enewetak. Comparative figures were: BAFS, $\bar{x} = 173.4$ mm, range $= 165–181$ mm, SE $= 0.6$, $n = 36$ adults and 7 juveniles; Enewetak, $\bar{x} = 171.9$ mm, range $= 164–179$ mm, SE $= 0.7$, $n = 4$ adults and 27 juveniles. Findings for the netted birds were in close agreement with the preceding results: $\bar{x} = 172.6$ mm, range $= 163–182$ mm, SE $= 0.6$, $n = 62$ adults; and not significantly different ($P > 0.35$ for both comparisons). In all of the foregoing samples, only wings with fresh, unworn outer primaries were included (i.e., juveniles in the fall and early winter before their primaries become worn, and adults after completion of primary molt). Thus, the proportions of adults and juveniles sampled do not reflect actual age ratios in the populations (though juveniles were more abundant at Enewetak as compared to BAFS, see beyond). Wing lengths of P. fulva from various regions including Hawaii, Siberia, and western Alaska were reported by Ridgway (1919), Conover (1945), Vaurie (1964), Dement'ev et al. (1951), Portenko (1972), Prater et al. (1977), Connors (1983), and Cramp and Simmons (1983). Geographic affinities are reasonably distinct since birds on Alaskan breeding grounds tend to have longer wings than birds on Siberian ranges. For example, Vau-

rie's means were about 171 mm ($n = 46$) and 166 mm ($n = 32$), respectively. Dement'ev et al., Portenko, and Prater et al. found Siberian P. fulva to have even shorter wings with means from 158–164 mm. Since our figures represent flattened wings (with primaries straightened) measured just after collection or on living birds, the readings obtained were the maximum possible. After correction for shrinkage of museum specimens (about 2%, Prater et al. 1977), the 171 mm figure mentioned above was nearly identical to our means. This relationship suggests that the plovers we collected at BAFS and Enewetak were of Alaskan origin. In contrast, plovers at Wake Island had shorter wings resembling Siberian birds (Johnston and McFarlane 1967). With allowance for shrinkage, wing lengths from other specimens collected in Hawaii (Ridgway, Conover) matched our results closely.

Premigratory weight gains occurred in all adults. With juveniles, however, some fattened and others did not. The former acquired various degrees of breeding plumage (many had complete breeding coloration) and migrated with the adults, the latter retained basic body plumage and oversummered on the wintering ground. Two juveniles "scheduled" to oversummer were collected, one each during the Premigratory and Migratory Departure periods. These birds weighed 110 g and 124 g, respectively; both were excluded from the findings shown in Table 2. Of the three premigratory juveniles represented in the table,

TABLE 2. Extended.

Mid- to Late Winter 18 Dec 1979–19 March 1980 Hawaii n = 6			Premigratory period 9–16 April 1980[c] Hawaii n = 3			Migratory Departure 23–27 April 1980[d] Hawaii n = 6		
$\bar{x}$	(Range)	SE	$\bar{x}$	(Range)	SE	$\bar{x}$	(Range)	SE
126.7	(114–146)	4.4	138.7	(126–158)	8.0	177.2	(158–192)	4.4
15.1	(7.1–31.2)	3.3	28.5	(18.1–39.3)	5.0	57.4	(44.5–70.7)	3.6
111.6	(106.9–120.0)	1.9	110.1	(107.9–118.7)	3.6	119.7	(101.6–130.5)	3.6
74.2	(68.7–81.6)	1.7	74.7	(72.8–81.2)	2.7	80.3	(68.5–87.5)	2.3
52.5	(42.5–69.5)	3.4	63.9	(53.2–76.8)	5.6	96.9	(87.5–109.7)	3.3
37.4	(33.6–44.0)	1.4	35.4	(33.7–37.5)	0.9	39.4	(33.1–43.0)	1.4
11.5	(6.1–21.4)	2.1	20.2	(14.4–24.9)	2.5	32.4	(25.4–36.8)	1.7
27.4	(14.2–44.9)	4.1	43.6	(34.1–51.2)	4.1	59.0	(50.8–64.5)	2.1
58.8	(52.4–62.7)	1.3	54.1	(51.4–57.8)	1.6	45.3	(42.9–50.0)	1.0
66.4	(60.9–68.6)	1.0	67.8	(67.5–68.4)	0.2	67.1	(65.3–67.9)	0.4
3.1	(2.3–4.1)	0.2	4.4	(2.9–5.4)	0.6	4.8	(3.8–6.2)	0.3
17.1	(8.1–35.0)	3.6	24.9	(14.4–38.8)	5.9	32.4	(16.5–52.2)	5.1

pattern has remained remarkably constant with departure typically near the end of April. The birds in this sample had well-developed fat stores and alternate plumages. Hence, all these juveniles were preparing to migrate, none to oversummer (see text).
[c] All weights in grams.
[f] All body components and calculations above include the liver.

one individual (weighing 126 g) was of questionable status and probably would have oversummered. Because of this uncertainty, we include the small sample of premigratory juveniles in Table 2 for general interest only and will say little more about them.

Sampling of plovers at Enewetak was limited to late November. Chronologically, we have no BAFS specimens (i.e., carcasses analyzed for body components) directly comparable to the Enewetak birds. Nonetheless, certain comparisons were desirable (especially between adults), and for these we used the two BAFS samples which bracket the Enewetak sample (i.e., the Fall Arrival and Mid-to Late Winter periods, Tables 1 and 2). Most comparisons between Enewetak and BAFS juveniles were avoided because our samples consisted of growing birds (see beyond) collected at dissimilar times. For convenience, we show the Enewetak results as Early Winter in Tables 1 and 2. By doing this, we do not mean to imply that these data are representative of BAFS birds at that point in the wintering cycle. While there were many similarities between the two groups, there were also important differences which will be described later.

We did not measure pectoral muscle mass in our specimens (these data also were unavailable for the Wake Island birds examined by Johnston and McFarlane 1967). It is reasonable to assume that relative pectoral muscle development varied directly with fat-free dry weights, however, we are unable to quantify the precise relationship.

TOTAL WEIGHT

We found considerable individual variation in total weight during Fall Arrival (Tables 1, 2; Fig. 1). Thereafter, no collecting was done at BAFS until 18 December. This was intentional since we were concerned that continued disturbance might cause birds (especially juveniles) to leave the area and seek residence elsewhere. Thus, we lack detailed measurements of body composition at BAFS during October, November, and early December. The total weights of the 12 birds netted during this period (Early Winter, Fig. 1), partially fill this void. Since all birds for banding were captured at or before dawn (see Methods), they had not fed prior to being weighed. In contrast, the collected specimens (including Enewetak birds) were generally obtained later in the day, often in the afternoon. Lloyd et al. (1979), Schick (1983), and Davidson (1984b) showed weight losses in newly caught shorebirds on the order of 2.5–3.0% of body weight over a 1- to 2-hr period. Our captives were held for similar lengths of time; thus, the weights in Figure 1 were depressed in comparison to undisturbed birds. Lacking actual measurements of this variable, a 3% correction factor seemed a conservative estimate of the combined effects of netting stress and inability to feed. On this assumption, the actual total weights of plovers sampled during Early Winter (Fig. 1) ranged from about 99–118 g.

An upward adjustment of 3% applied to the

remainder of Figure 1 produced weights consistent with the values shown in Tables 1 and 2, except for two birds each weighing 190 g (195.7 g after correction) which were captured prior to mid-April (during the Premigratory Period, Fig. 1). Birds of similar weight were not found in the collected sample until nearly the end of April (Tables 1 and 2). Compared to the Early Winter sample, the Mid-Winter birds (Fig. 1) showed significant weight gains ($t = 4.87$, $P = 0.0001$). While a few birds appeared to gain additional weight as the winter progressed, most remained about the same through mid-March and mean weights for the Mid-Winter and Late Winter samples were not significantly different ($P = 0.581$). A trend toward premigratory fattening was apparent by late March with Early Spring birds significantly heavier than Late Winter birds ($t = 2.48$, $P = 0.016$), followed by dramatic weight gains into April (Fig. 1). The onset of rapid weight increase was less clear among collected birds since we lacked a sample from late March, but major weight gains were evident during the Premigratory and Migratory Departure periods (Tables 1 and 2). At Migratory Departure, there was no significant difference between the weights of adults and juveniles ($P = 0.477$).

FAT CONTENT

Mean total fat levels ranged from about 10–17 g during the Fall Arrival and Mid- to Late Winter periods (Tables 1 and 2). The higher mean fat content of fall juveniles (16.9 g) as compared to fall adults (9.9 g) was not statistically significant ($P = 0.102$). At migration there was no significant difference between the fat stores of adults and juveniles ($P = 0.690$). We found no evidence of sex-related variation in total fat levels.

As mentioned before, most birds began premigratory fattening toward the end of March. At migration 1 month later, their winter fat stores had increased approximately four-fold. Over the entire wintering cycle at BAFS, the fattest bird (a juvenile with 70.7 g of lipids collected during Migratory Departure) was about 21 × fatter than the leanest specimen (an adult with 3.3 g of lipids collected during Fall Arrival). Expressed as mean percent of total weight, fat averaged around 8–15% from the fall through most of the wintering season (including the Enewetak birds), and increased to about 32% at the time of migration. Fat as a percent of total dry weight ranged from means of about 21–32% (including Enewetak

specimens) from fall through 19 March, 44–48% in early April, and 58–59% at migration in late April (Tables 1 and 2). Comparing adults and juveniles, we found no significant differences ($P > 0.05$ for all tests) in total fat (expressed as percentages of total weight and total dry weight) at any period from Fall Arrival through Migratory Departure.

Fat content was closely related to both total fresh weight ($r = 0.92$, $P < 0.001$; $r^2 = 0.85$) and total dry weight ($r = 0.97$, $P < 0.001$, $r^2 = 0.95$). The respective equations for calculating fat reserves are: $F = 0.64(FW) - 63.14$, where F is fat in g, and FW is fresh weight in g; and $F = 0.88(DW) - 31.53$, where F is fat in g, and DW is total dry weight in g. The regressions are shown in Figure 2.

RELATIONSHIPS BETWEEN FAT-FREE WEIGHT (FFW), FAT-FREE DRY WEIGHT (FFDW), AND WATER CONTENT

The lowest FFWs and FFDWs of the wintering season were found during Fall Arrival (Tables 1 and 2). In both adults and juveniles, the fall means were significantly lower ($P < 0.05$ for all tests) than the means for subsequent periods. Comparisons between the two age classes indicated significantly higher FFW and FFDW in fall adults, $t = 3.46$ ($P = 0.003$), and 2.11 ($P = 0.048$), respectively; but no differences during the remainder of the wintering cycle. We interpreted the higher FFDW in adults as indicating greater physical maturity. Among fall juveniles (collected soon after their arrival), the FFW of only one specimen exceeded 100 g (107.1 g), the others were 83.6, 85.5, and 90.3 g. Since the birds still contained reserve fat, it was unlikely that these low FFWs reflected stress during the first migration (this is not to say that such stress is unimportant, it may have significant impacts on juveniles, see beyond). Rather, such results along with low FFDWs (Table 2) suggest that fall juveniles are not yet fully developed when they arrive on the winter range, and that their pectoral muscles and other body components undergo further growth subsequent to arrival.

Water as a percentage of FFW was nearly constant in BAFS specimens throughout the wintering season, with mean values ranging from about 65–68% (Tables 1 and 2). Comparisons of the means between successive sample periods revealed no significant differences ($P > 0.05$ for all tests) among juveniles, one significant differ-

ence among adults (Mid- to Late Winter birds as compared to Migratory Departure birds, $t = 2.76$, $P = 0.010$), and no differences when comparing adults and juveniles. By contrast, Enewetak adults and juveniles contained significantly less water (about 62% of FFW, Tables 1 and 2) than BAFS birds ($P < 0.05$ for all tests). Lacking additional collections from Enewetak, we do not know if the lower value typifies the entire season there.

Since water content on a relative basis did not change appreciably through the season in BAFS birds, increasing mean FFWs subsequent to Fall Arrival reflected growth of organic body mass or FFDW. From Fall Arrival to Migratory Departure, mean FFDWs increased 12.5% in adults (from 35.2 g to 39.6 g, Table 1), and 23.1% in juveniles (from 32.0 g to 39.4 g, Table 2). In each case, this was statistically significant growth, $t = 3.41$ ($P = 0.003$), and 3.62 ($P = 0.007$), respectively. The relationship between water and FFDW in BAFS specimens was approximately 2 g water/g FFDW. Enewetak birds contained about 1.6 g water/g FFDW.

LIVER WEIGHT AND FAT CONTENT

Although we found much individual variation in liver weight and fat content, mean values were reasonably well correlated with seasonal changes in total body weight and fat stores. Among BAFS birds, mean liver weights and mean fat content of the liver (expressed as percent fat of dry weight) were least during Fall Arrival, intermediate from Mid- to Late Winter, and highest in the Premigratory and Migratory Departure periods (Tables 1 and 2). Mean liver weights in fall adults and juveniles were significantly lower when compared to each subsequent period in the wintering cycle ($P < 0.01$ and <0.05, respectively, for all tests). The mean fat content of livers from fall adults was significantly lower than any subsequent value from later sample periods ($P < 0.01$ for all tests). While the comparable figure for fall juveniles (11.7%, Table 2) was lower than all later samples, the only significant difference was between the Fall Arrival and Migratory Departure periods ($t = 2.85$, $P = 0.021$). Comparisons between the means of adults and juveniles in each respective sample period (including the Enewetak sample) revealed no age-related differences in either liver weight or fat content. The low mean fat levels found in the livers of Enewetak birds (6.0% in juveniles and 7.0% in adults, Ta-

bles 1 and 2) differed significantly from BAFS birds ($P < 0.05$ for all tests).

Analyses of relationships between the liver and other body components ($n = 131$) produced the following equations: liver lipids (g) = 0.013 × total body lipids, excluding liver lipids (g) − 0.067, $r = 0.73$; % lipids in dry weight liver = 0.58 × % lipids in dry weight body, excluding liver lipids −4.00, $r = 0.72$; and liver weight (g) = 0.02 × body weight, excluding liver (g) + 0.91, $r = 0.49$.

FLIGHT RANGES

The estimation of fat-free weight (basic to the flight range formulae, see Methods) is beset with various complicating factors such as possible dehydration just prior to migration, partial catabolism of protein reserves during extended flights, and marked short-term variations in liver and gut weights (Davidson 1983, 1984a). In arriving at an estimate, we used Johnston and McFarlane's prior work (1967) plus data from Enewetak and the Migratory Departure period at BAFS (Tables 1 and 2). Johnston and McFarlane collected golden-plovers on Wake Island in August, December, and April; from these data (divided according to sex) we calculated water as a percent of FFW in each of their sample groups. In August and December, means ranged from 65.6 to 67.1%, almost identical to our findings (Tables 1 and 2). But in April, the water content of Wake plovers dropped substantially below BAFS birds, decreasing to 59.1 and 60.1% in females and males, respectively. Although Johnston and McFarlane did not mention the possibility, it appears that their April specimens were undergoing premigratory dehydration. Similar findings in other shorebirds (McNeil 1970, Davidson 1984a) indicate that dehydration may be an important adaptation to lessen weight, thus increasing flight range and/or energy stores at the migratory destination. (We were puzzled by Summers et al. 1987 who reported "no evidence of pre-migratory dehydration" in Sanderlings [*Calidris alba*], yet their data show water as a percent of FFW ranging from 62–65% over the period 31 July–29 January, then decreasing to 57–58% from 18 March–2 May.) The specimens collected at Enewetak had varying degrees of dehydration with water content as low as 55.7% of FFW, averaging about 62.0% (Tables 1 and 2). These findings probably reflected sampling of intramigrants enroute further south and/or birds

TABLE 3.   Body composition of selected specimens during the Migratory Departure period.

Specimen number, age and sex, date collected	Total weight (g)	Total lipids (g)	Total water (g)	FFW (g)	Water (%FFW)	FFDW (g)	Wing length (mm)
68, JvM, 23 April	175	44.5	87.5	130.5	67.0	43.0	171 (w)[a]
70, AdF, 23 April	188	68.2	80.7	119.8	67.4	39.1	167
71, AdM, 23 April	187	60.0	84.2	127.0	66.3	42.8	171
72, JvF, 23 April	192	70.7	82.3	121.3	67.8	39.0	172 (w)
73, JvM, 23 April	184	61.1	82.6	123.0	67.1	40.3	177 (w)
77, AdM, 27 April	152	48.4	64.3	103.6	62.1	39.3	176
79, AdF, 27 April	172	52.0	75.8	119.9	63.2	44.2	173
81, JvM, 27 April[b]	124	11.5	76.4	112.5	67.9	36.1	170 (w)

[a] The symbol (w) indicates worn primaries characteristic of juvenile birds in the spring (see text). When measuring a wing, we made no attempt to estimate how much of the longest primary was worn away, thus these figures are inaccurate to the extent of feather wear.
[b] This specimen was not accumulating fat reserves and probably would have oversummered at BAFS.

otherwise moving about the scattered atolls of this region (see further discussion beyond). The Wake Island and Enewetak data clearly indicated that water content in *P. fulva* can fall substantially below the levels found in BAFS specimens. Furthermore, these adjustments appear to be unrelated to either the availability of fresh water in the environment or to temperature stresses. Examination of weather records from Wake Island and Kwajalein Atoll (located near Enewetak) disclosed the following: (1) Wake Island is much drier than Enewetak. Mean annual rainfall on Wake over the period from 1936–1983 was 92.48 cm, and on Kwajalein from 1945–1983 it was 260.58 cm. Thus, puddles of water (from which wintering plovers often drink) would be less frequent on Wake. Nonetheless, water content was high in the birds collected by Johnston and McFarlane during August and December. (2) In December 1964 (when Johnston and McFarlane collected their midwinter sample) the rainfall on Wake Island was 4.24 cm, in April (spring sample) it was 9.35 cm. Therefore, birds were dehydrated under conditions of relatively high rainfall and vice versa. (3) Rainfall on Kwajalein in November 1978 was 41.05 cm. Thus, the dehydrated birds we collected at Enewetak were taken during a very wet period. In fact, our field notes contained several references to heavy and prolonged rains. (4) Mean annual temperature (over the period 1948–1983) was almost identical for Wake and Kwajalein (26.7° and 27.8°C, respectively), and average temperatures were nearly constant from month to month. Such relationships are consistent with dehydration as a physiological process rather than an aberration brought on by climatic fluctuations.

In Table 3, we present data for some of the birds collected during the Migratory Departure period with specimens selected to show the overall range of variation found in this group. Relationships between FFW and relative body size (as indexed by wing length and FFDW) were inconsistent, leading us to conclude that the primary variable influencing FFW was relative water content of the individual. Presumably, plovers throughout the Pacific winter range share similar physiological responses to migration. Given the dehydrated state of various Wake Island and Enewetak specimens, we would expect comparable adjustments in the plovers at BAFS. Dehydration to 60% or less of FFW prior to spring departure seems likely. Specimens 77 and 79 (Table 3) were probably demonstrating this, thus approaching 100 g FFW at departure. On this basis, we selected 105 g FFW as a reasonable estimate for BAFS birds and used this figure when calculating their spring flight ranges. Intraspecific variations in FFW (both geographic and seasonal, Davidson 1983) are likely across *P. fulva*'s vast range. The extent of this variability is unknown, and measurements are needed during migratory departure from a number of sites on both the breeding and wintering grounds. Lacking such information, we applied the 105 g FFW factor in other calculations including some for fall migrants. Obviously, future studies may produce refinements in estimating FFWs for specific regions and populations.

Measuring the exact body compositions of plovers at the moment of migratory departure is probably impossible, and an approximation from specimens very near migration seems the only alternative. Such an effort is shown in Table 4 which is based on three assumptions: (1) premigratory dehydration reduced the average FFW

TABLE 4. Body composition and flight ranges in selected specimens after premigratory dehydration.[a]

| Specimen number | Total weight (g) | Total lipids (g) | Total water (g) | Water (% FFW) | Flight range[b] (km) | | Possible destinations[c] | | | |
| | | | | | | | Aleutians (3,860 km) | | Kuskokwim River Delta, Copper River Delta (4,500 km) | |
					(Dav.)	(S&W)	(Dav.)	(S&W)	(Dav.)	(S&W)
68	150	44.5	62.5	60	4,634	5,379	7.6 g (17%)	12.5 g (28%)	1.3 g (3%)	7.1 g (16%)
70	173	68.2	65.9	63	6,632	7,671	28.6 g (42%)	34.1 g (50%)	21.8 g (32%)	28.0 g (41%)
71	165	60.0	62.2	59	5,960	6,901	21.0 g (35%)	26.4 g (44%)	14.4 g (24%)	21.0 g (35%)
72	176	70.7	66.0	63	6,879	7,953	31.1 g (44%)	36.0 g (51%)	24.7 g (35%)	30.4 g (43%)
73	166	61.1	64.6	62	6,045	6,999	22.0 g (36%)	27.5 g (45%)	15.9 g (26%)	22.0 g (36%)
77[d]	152	48.4	64.3	62	4,981	5,781	10.9 g (23%)	16.1 g (33%)	4.7 g (10%)	10.7 g (22%)
79	157	52.0	60.9	58	5,264	6,103	14.0 g (27%)	19.2 g (37%)	7.8 g (15%)	13.5 g (26%)

[a] Specimens are the same as in Table 3, except no. 81 has been omitted since it was not undergoing premigratory fattening.

[b] Calculated according to the Davidson (Dav.), and Summers and Waltner (S&W) formulae (see Methods). FFW assumed to be 105 g, and flight speed 104.7 km/hr.

[c] Each area is a possible first stop for spring migrants assuming a more or less directly north flight, the approximate distances from BAFS are shown. A shorebird flyway between Alaska and Hawaii is reasonably well-known, but further studies are needed (Baker 1951, Thompson 1973, Kloeckner et al. 1982, Williams et al. 1986). Alaska breeding grounds are likely for BAFS plovers (see text). The two numbers in each column are the approximate percent of total lipids and the approximate grams of lipids remaining at the completion of the flight. These figures were derived from the ratio between the actual distance flown (either 3,860 or 4,500 km) and the calculated flight range of the individual. The Kuskokwim and Copper river deltas are about equidistant from BAFS. The former is at the southern end of P. fulva's breeding range in Alaska (AOU 1983), the latter is a major spring staging area for shorebirds (Isleib and Kessel 1973, Senner 1979) which may be significant as a landfall and fattening site for trans-Pacific migrants. At BAFS (and elsewhere along the eastern shore of Oahu), migratory departure occurs in late April. Subsequent events during migration are unclear. Whether the birds aggregate on staging areas (as implied by Isleib's 1979 observations in the Copper River Delta region, also see Sauer's 1962 speculations) or return more or less directly to the breeding grounds (perhaps resting and feeding enroute as conditions permit) is unknown. Except for Isleib's report, there are no other spring records suggesting major plover aggregations in Alaska (R.E. Gill, pers. comm.). This lack of records, and the fact that most littoral habitats along the eastern Bering Sea shorebird corridor are usually ice-fast during spring migration (Gill and Handel 1981), favor direct return. The matter awaits further investigation.

[d] In this specimen it was assumed that premigratory dehydration had already occurred, and the bird's actual FFW (103.6 g, Table 3) was used in the calculation of flight range.

to 105 g at departure, (2) no further accumulation of fat occurred during the dehydration period, and (3) the average flight speed during migration was 104.7 km/hr (65 mph). A bird's total weight after dehydration is its original total weight (Table 3) minus water lost in achieving a FFW of 105 g. Thus, our heaviest bird (no. 72 at 192 g, FFW of 121.3 g) would lose 16.3 g of water and depart on migration as a 176-g bird containing 70.7 g of lipids. From the latter parameters, the projected flight ranges for this individual (Table 4) were 6,879 km (Dav.) or 7,953 km (S&W). With this capacity for flight, specimen 72 could have migrated to the Aleutian Islands, Kuskokwim River Delta, or Copper River Delta, and arrived at any of these locations with considerable reserves of fat. The same general findings also apply to specimens 70, 71, and 73. While the remaining specimens (nos. 68, 77, and 79) could have migrated, they would have reached landfall with lesser reserves (Table 4). Clearly, these predictions would be modified should the underlying assumptions change. If additional fat gains occurred, or if flight speed was faster or slower, flight ranges would vary accordingly.

DISCUSSION

WINTER BEHAVIOR

In earlier work, we described certain behavioral features of the plovers under study at BAFS (Johnson et al. 1981). Some of these findings, combined with more recent observations, are relevant to the fat cycle. The population consists of both territorial and nonterritorial birds. (A similar duality occurs to varying degrees in other shorebirds, for a review of this phenomenon see Myers et al. 1979.) Territorial plovers occupy and defend the same territories (the latter are often relatively large ranging to about 4,000 m²) daily for the entire wintering season, using them primarily as feeding sites. Many territories are on lawns, others are along roadsides, in groves of ironwood trees (Casuarina spp.), and at the edges of unused runways. Upon returning in the fall, each territorial bird typically reoccupies the identical territory defended in the previous season. Like the Grey Plover (P. squatarola) on wintering grounds in England (Townshend 1985), selection of either the territorial or nonterritorial mode of behavior appears to occur during the juvenile bird's first wintering season. Thereafter, the individual's behavior likely remains fixed for

life (i.e., either territorial or nonterritorial in all subsequent wintering seasons). At least one-half of the plovers resident at BAFS during the 1979–1980 season (the period over which the specimens for fat analyses were collected) were territorial. Nonterritorial birds remain spatially separated from territorial individuals, foraging and performing other activities communally. Furthermore, they have occupied the same communal sites (primarily unused runways) annually. With disturbance (especially human activities on the study area), territorial birds leave their territories for varying lengths of time and join with groups of nonterritorial birds. This intermingling sometimes results in large aggregations on sites safe from disturbance. In the fall, adult plovers arrive at BAFS from mid-August through mid-September, juveniles do not appear until the end of September with most arriving in October. Annual survival and site fidelity from 1980 through 1987 (based on return rates of color-banded birds) averaged 82%. Since almost all netting was done in the late winter and early spring, most of the birds banded were successfully established residents.

AGE-RELATED PHENOMENA ON THE WINTER RANGE

During the Fall Arrival period, some adult birds were lean, others relatively fat (Table 1). Similar findings were reported by Henshaw (1902, 1910) and Johnston and McFarlane (1967). The factors most likely involved in this variation are individual differences in premigratory fattening, and weight losses following arrival. While we cannot quantify the energetics of the second variable, individuals probably lose weight in proportion to the costs associated with the onset of wintering behaviors combined with molting. Territorial adults engage in what appears to be an energetically expensive process whereby territories are reestablished and defended. At first this involves bouts of prolonged and vigorous fighting over several days until boundaries are settled. Thereafter, the more violent aggressive encounters decrease markedly and for the remainder of the season are replaced by less agonistic behaviors at territory edges (Johnson et al. 1981). While not so dramatic, the interactions of nonterritorial birds as they reestablish intraflock relationships entail unknown energy expenditures.

For inexperienced juvenile plovers, the energy costs associated with the first southward migra-

tion and with the competition necessary to es-tablish residency on the wintering grounds, may exceed the energy available and become major causes of mortality. The high survival rate of banded birds indicates relatively slow turnover following establishment of residency on the win-tering grounds, and suggests that annual mor-tality involves mostly juveniles. Such losses have been observed by U.S. Fish and Wildlife Service biologists (pers. comm.) at Tern Island (approx-imately 24°N, 166°W) in the northwestern Hawaiian Islands where dead and dying plovers occur regularly in the fall and early winter. Work-ers at Tern salvaged 18 of these birds for us in 1981 and 1982, 15 of which proved to be ju-veniles. All of the specimens were extremely emaciated, of 13 birds weighed (10 juveniles, three adults) the mean was only 54 g (range 50.0–63.5 g). We extracted lipids from seven of the specimens (six juveniles, one adult) finding small quantities of structural lipids only ($\bar{x} = 0.97$ g, range $= 0.77$–1.35 g), there were no reserves of stored fat. Extensive protein catabolism was ev-ident since the pectoral muscles and internal or-gans were dramatically reduced (pectoral muscle index $= 0$, see Davidson and Clark 1985). The adult birds ranged from 53–63 g at death, the juveniles from 50–63.5 g. Relative to FFWs the weight losses preceding death were about 40–50% in adults (assuming normal adult FFW to be 105 g), and around 30–44% in juveniles (as-suming 90 g FFW since these birds were not yet fully grown). In various other shorebirds dying from starvation, lean weight losses ranged from 21–42% (Davidson 1981). According to the bi-ologists at Tern Island, young plovers either ar-rive in emaciated condition and die shortly thereafter, or gradually waste away after arrival. In the latter situation, it appears that juveniles are unable to compete successfully with estab-lished birds for the limited resources available. One of us (Bruner) made observations at Tern Island in September 1985 prior to the arrival of that season's crop of juveniles. He found the available habitat filled by about 80 birds many of which appeared to be territorial.

To varying degrees, the situation at Tern may reflect first-winter conditions throughout the Pa-cific. Under the best of circumstances (BAFS, for example, has extensive lawns with abundant in-sects, whereas such habitats are lacking at Tern Island), juveniles that survive their initial mi-gration must then compete with adults already established on the wintering ground. It is notable that Johnston and McFarlane (1967) found no cloacal bursae in any of the specimens they col-lected on Wake Island. While reduced bursae could have been overlooked in winter and spring birds (for additional information concerning the bursa in *P. fulva*, see Johnson 1973), their find-ings suggest habitats filled mostly with adults (as at Tern) wherein survival would be difficult for juveniles. By deferring the replacement of ju-venile primaries until the second wintering sea-son (Johnson and Johnson 1983), young birds are likely better adapted to survive their first season. Aside from energy considerations (i.e., growth of new remiges), missing primaries might impair agility making interactions with resident adults more stressful and/or decrease overall mo-bility on the winter range. For survivors of the first winter, energy limitations may preclude pre-migratory fattening and result in oversummering behavior (Johnson 1985). Though it seems pos-sible that oversummering might enable some birds to acquire territories while residents are away, this has never been observed at BAFS. Since 1980, we have monitored about 10 over-summering plovers each season. Typically, the group behaved gregariously with birds dispersed in a loose flock. There was no evidence of in-dividuals attempting to defend specific areas. The flock often foraged on vacated territories during the summer, but was displaced from these sites when territory "owners" returned in the fall.

COMPARISONS OF PLOVERS FROM WAKE, BAFS, AND ENEWETAK

Johnston and McFarlane (1967) made observa-tions and collections in the fall (22–30 August 1964), midwinter (21 December 1963–5 January 1964 and 19 December 1964–9 January 1965), and spring (11–26 April 1964). Although their August visit was too brief for a thorough de-scription of fall migration, it was evident that Wake Island (relatively isolated at approximate-ly 19°N, 166°E) is a stopping point visited by plovers enroute further south. The birds that re-mained as winter residents "dispersed over the island and occupied almost all available habi-tats." Therein they became solitary, "rarely were more than two seen together," and established territories which were "vigorously defended." In addition to its complement of territorial plovers, Wake Island had "a continuous flux of individ-uals and small flocks" during the midwinter pe-

riod. Among the transients were several species of shorebirds including golden-plovers. The visitors "seldom remained very long and might represent inter-island movements of many wintering species."

Like Wake Island, BAFS also appears to host plovers enroute elsewhere. In earlier work (1979–1980 wintering season, see pers. comm. to Kloeckner et al. 1982) we failed to detect this. But frequent census counts since then (through spring 1987) have peaked in the fall, leveled off through the winter, then peaked again in the spring. We do not know if these peaks represent travelers passing to and from winter ranges elsewhere in the Pacific, or birds wintering in the Hawaiian Islands. Radar studies suggest the former (Kloeckner et al. 1982, Williams et al. 1986), but the expansive runways and lawns at BAFS could attract plovers associated with regional wintering areas as well. Unlike Wake, we have never observed any significant fluxes of plovers or other shorebirds during the winter months at BAFS. Following the fall peak, the wintering population (composed of previous residents plus juveniles that have established residency) remains stable until spring.

Based on the foregoing, it is likely that the collections from Wake contained both residents and transients, whereas the BAFS sample consisted primarily of residents. Weights of the August birds at Wake ($n = 11$ adults, migration of juveniles not yet underway), which averaged about 16 g heavier (with about 12.5 g more fat) than BAFS birds, probably reflect sampling of intramigrants during a stopover. In fact, Johnston and McFarlane commented about having taken these plovers from flocks which implied passers-by rather than returning residents. The December sample from Wake ($n = 12$, considered to be all adults, but see earlier comment regarding cloacal bursae) averaged about 130 g total body weight including 15 g fat. These values were almost identical to our findings (Mid- to Late Winter, Tables 1 and 2), and may indicate that mostly resident individuals were collected. Sampling of birds in the spring at Wake ($n = 27$, all classified as adults which we believe unlikely) coincided with our Premigratory and Migratory Departure periods. Body weights (mean about 153 g, range = 121.9–192.1 g) and fat stores (fat content was measured in only 11 specimens, carcass components of the others were accidentally lost) were very similar to BAFS birds (Tables 1 and 2). Johnston and McFarlane divided the April sample into two categories: the heaviest individuals were considered residents or intramigrants with essentially complete fat stores, the others were premigrants still accumulating fat reserves. Our findings indicate that a third group consisting of juveniles (weighing around 120 g) "scheduled" to oversummer also was present. Johnston and McFarlane did not consider the oversummering option noting that plovers were "generally absent from early June to late July" at Wake Island. However, this would not preclude Wake birds from oversummering elsewhere. Flight-range predictions (Fig. 3) show that 120-g plovers have more than enough mobility (approximately 1,675 km, Dav.; 1,955 km, S&W) to reach other atolls. The northern fringe of the Marshall Islands is about 900 km south of Wake, and Enewetak Atoll (where substantial numbers of oversummering plovers have been observed, Johnson 1979) is about 1,100 km to the southwest.

Enewetak is a coralline atoll similar to Wake Island, except that it is much larger consisting of some 40 islets encircling a lagoon approximately 20 nautical miles in diameter. During our November visit, we observed solitary (presumably territorial) plovers in grassy areas adjacent to the runway on the main islet and in low vegetation on several other islets. We were unable to make a thorough survey of the atoll, but it appeared that Enewetak (like Wake) holds a complement of territorial birds wherever there is suitable habitat. In addition to these birds, we also observed flocks of plovers moving about the atoll (comparable to the "continuous flux" noted by Johnston and McFarlane at Wake Island). Because of military restrictions, we were unable to obtain selective samples of territorial individuals. Instead our collecting had to be done in specified locations where we generally took birds opportunistically from flocks that were passing by or that alighted. The range in total weights (100–160 g) and fat stores (5.5–39.4 g, Tables 1 and 2) of our samples suggested birds of differing physiological and behavioral states. In other words, residents and transients, the latter being visitors from nearby atolls and/or migrants that had stopped while enroute elsewhere. The possibility that our collection included migrants is supported by observations in New Zealand and Australia where fall arrival of golden-plovers occurred through the end of November (Parish et

al. 1987). Many Enewetak specimens had relatively low water content (as described previously) which would enhance mobility. To what extent plovers wintering on Enewetak (particularly nonterritorial individuals) might travel from islet to islet and/or visit neighboring atolls is unknown. Flight ranges for Enewetak birds of average weight (Tables 1 and 2) were about 1,490–1,720 km (Dav.) or 1,740–2,000 km (S&W). Since there are a number of landfalls within 500–700 km, interatoll flights would be possible and might permit exploitation of food resources over a relatively wide region. At BAFS, territorial birds were very site faithful and showed no pattern of irregular occurrence suggesting movements to and from other areas. It was possible that such movements of nonterritorial birds (intra-island on Oahu or to neighboring islands) escaped detection.

Slightly more than half of the birds obtained at Enewetak (27 of 52) were juveniles. In contrast, among the 211 plovers handled at BAFS from 1979 through 1987 (both banded and collected) adults predominated by about 3:1. Since our collecting on Enewetak was essentially random and often involved flocks, it appeared that these groups contained many young individuals. Perhaps juveniles respond to competition from established residents by flocking and wandering during the first wintering season. Such behavior might account for the fluxes mentioned before. Most of the juveniles collected at Enewetak were in good condition, 13 of the 27 weighed in excess of 120 g. This reversal from the previously described situation at Tern Island suggests more abundant food resources at Enewetak.

FAT RESERVES

Because of the lost data mentioned above, Johnston and McFarlane were unable to plot the fat/body weight relationship beyond about 165 g total body weight. From the information in hand (representing 34 birds), they calculated a regression and then projected it linearly so as to estimate the fat content of their heaviest (i.e., lost) specimens which ranged to 192.1 g. We can now expand upon these findings since we have a considerably larger sample (133 birds) complete to 192 g fresh weight (Fig. 2). Our regression differs from the Johnston and McFarlane expression in that its slope is less steep. The two lines intercept at about 140 g, our's predicts more fat/unit body weight below this point and less above it. For

example, in a 190-g bird our equation would estimate fat at about 58 g, their's at about 84 g. Premigratory dehydration (evident in the Johnston and McFarlane April specimens, less evident in our's) is an important factor when comparing the two equations. This phenomenon lowered total body weight relative to fat load, in effect steepening the overall regression curve for Wake Island birds. Considering dehydration, it is possible that the Johnston and MacFarlane expression (fat $= 1.12 \times$ body weight $- 129.3$) gives the better estimate of fat reserves at migratory departure.

Shorebirds wintering in northern latitudes often exhibit a midwinter peak in fat stores ("insurance" against the vagaries of weather and food supply), followed by fat losses until premigratory fattening in the spring (Evans and Smith 1975, Dugan et al. 1981, Davidson 1981, McEwan and Whitehead 1984). Although less is known about the physiological responses of shorebirds to wintering conditions in other parts of the world, winter fattening generally does not occur under more favorable climatic conditions wherein the probability of needing reserves is minimal (for further discussion and references see Dick and Pienkowski 1979, also Pienkowski and Evans 1984). There was no midwinter lipid peak in the BAFS plovers, the birds remained relatively lean until spring premigratory fattening (Tables 1, 2; Fig. 1). Since insects were abundant (Bruner, unpubl. studies) this pattern did not reflect seasonal food shortage. Instead, it suggests that the relatively constant tropical conditions afforded by Hawaii make insurance unnecessary. Furthermore, maintaining nonessential weight might be energetically disadvantageous and also increase the risk of predation (Dick and Pienkowski 1979). Predation is central to Lima's (1986) model in which winter fat reserves reflect "a trade-off between the risk of starvation and the risk of predation," the latter risk decreasing with leanness. We have no evidence of diurnal predation among BAFS plovers, aerial predators are absent and the abundant mongoose (*Herpestes auropunctatus*) appears to pose little or no threat. At night, however, the situation may be much different with potential impacts from rats, feral cats, and Barn Owls (*Tyto alba*).

Most premigratory weight gains occurred during the interval from late March through migration in late April. While we do not know the exact quantities of fat carried by departing birds,

the heaviest individuals collected contained approximately 70 g. Of this amount, 50 g (perhaps more) was accumulated over the 1-month period. This represented weight gain of approximately 1.7 g/day or 1.6% of FFW/day, which was similar to the fattening rate of Sanderlings (Summers et al. 1987) and toward the lower end of the range reported in several other shorebirds (1–7% of FFW/day, Pienkowski and Evans 1984). The highest lipid index (i.e., fat as a percent of total body weight) among our specimens was 37% before dehydration, 40% after (no. 72, Tables 3 and 4). Higher indices occur in *P. fulva* based on migrating plovers (see below) which were heavier than any weighed either in this study or by Johnston and McFarlane. (Max Thompson kindly provided the weights of 111 adult *P. fulva* captured during early fall 1964–1966 on St. George Island in the Pribilofs [some of these data also were used by Johnston and McFarlane 1967]. The birds were fattening on insect larvae produced in the remains of harvested seals [Thompson 1973], six weighed in excess of 210 g with the heaviest individual an astounding 251.5 g. It seems likely that such weights are atypical for *P. fulva*, being the result of unusually abundant food then present on St. George.)

SEASONAL CHANGES IN FFDW

Various shorebirds (including *P. fulva* on Wake Island) demonstrated a seasonal pattern wherein FFDW was least in the fall then increased to a maximum by spring (Johnston and McFarlane 1967, McNeil 1970, Evans and Smith 1975, Davidson 1981, Summers et al. 1987). For juvenile plovers at BAFS the increase was correlated with growth and development during the first winter, in adults other factors appeared to be involved. Johnston and McFarlane showed that FFDW increased from about 38 g in August (all adult plovers) to about 46 g in April (probably some juveniles in the sample, see earlier comments). Assuming that FFDWs in adults and juveniles were equal in the spring on Wake (as we found at BAFS), these values reflect approximately 21% growth in the adults from fall to spring or nearly twice that of BAFS adults. Johnston and McFarlane analyzed the FFDWs of males and females separately for each of their three sample periods. In August and December, their specimens had higher FFDWs than comparable BAFS birds, but limited sample sizes precluded *t*-tests. For April, we were able to make statistical comparisons by dividing our specimens (Tables 1 and 2) according to sex and calculating a mean for each group. The results showed significantly higher FFDWs in both males and females from Wake Island ($P < 0.05$). The comparative means for BAFS and Wake birds, respectively, were: 40.7 g vs. 44.9 g in males ($n = 18$ BAFS, 7 Wake), and 39.3 g vs. 47.2 g in females ($n = 13$ BAFS, 4 Wake). Adults from Enewetak also had relatively high FFDWs (Table 1) which were significantly greater ($P < 0.05$) than the fall and winter BAFS samples.

Although we are unable to correlate these variations in FFDWs with specific adaptations, there are at least three possibilities: muscle hypertrophy for carrying additional weight (fat) over long distances, meeting protein requirements during flight, and need for reserve protein at the migratory destination. This last function is probably the most significant, with reserves having greatest importance in spring when birds are confronted with unpredictable weather and food supplies on the breeding grounds. In the fall, demands for premigratory muscle hypertrophy may be less since migrants usually return to winter ranges where conditions tend to be relatively stable from year to year. (For general discussions of these relationships with pertinent references, see Evans and Smith 1975, also Davidson and Evans 1988.) At BAFS the weather is predictably clement and insect prey appear to be abundant. Thus, it is probable that adults bound for BAFS show minimal muscle growth, and that their low FFDWs at arrival do not reflect migratory stresses but rather the favorable conditions to which they are returning. The situation is likely reversed in the spring, with higher FFDWs indicating less predictable circumstances upon arrival in the north. We do not know why the FFDWs of Enewetak and Wake Island plovers are higher than BAFS birds, though similar factors must be involved. Perhaps conditions on the breeding or wintering grounds vary enough between the sample groups to account for the difference. Obviously, FFDW on tropical Pacific ranges cannot be a function of severe winter weather as in Britain (Davidson et al. 1986). Therefore, if conditions on the winter range are involved at all, the effect must relate to other factors influencing food supply (mostly insects) such as soils and the nature of plant communities, and seasonal and geographic variations in rainfall. These variables often differ profoundly among atolls and from

atolls to high islands. With respect to the length of migratory flights, we pointed out before that plovers wintering in Hawaii probably migrate along a direct north-south corridor. Further south, however, the migrations become considerably longer and may involve more complex patterns. Possibly, some plovers wintering south of Hawaii follow the same elliptical route as Ruddy Turnstones: southward in fall from the Pribilof Islands to the central and south Pacific, northward in spring along the Asian coast (Thompson 1973, McClure 1974). Extensive movements are indicated by the recoveries of two plovers banded in the Pribilofs by Max Thompson and found in subsequent years on the east coast of Australia and in the Solomon Islands, respectively (unpubl. data, U.S. Fish and Wildlife Service, Bird Banding Laboratory). Unlike many other regions of the Pacific, BAFS is located relatively close to the breeding grounds. Also, the site appears to provide excellent habitat. Perhaps the lower FFDWs of plovers wintering there reflect this particular blend of circumstances. Such questions are in need of further study.

ESTIMATED FLIGHT RANGES

Because of the passerine-like metabolic rates found in shorebirds (Castro 1987, Kersten and Piersma 1987), existing formulae for prediction of flight ranges may require significant modification. It is possible that formulae incorporating relatively low flight metabolism values derived solely (Davidson 1984a) or in part (Summers and Waltner 1979) from nonpasserines produce overestimates, and that a flight metabolism expression based on passerines (Kendeigh et al. 1977) would be more satisfactory. Also, aerodynamic theory (Pennycuick 1975) as related to body streamlining, effects of wind during migrations, and other variables may prove fundamental to accurate determination of flight ranges (Davidson 1984a). With these reservations and pending further studies of shorebird metabolism, we have calculated ranges according to presently-used formulae.

In Figure 3 we show projected ranges for birds of various weights. Depending upon flight speed, the minimum body weights required for the BAFS-Aleutians route would vary from about 142–154 g (Dav.) or 136–147 g (S&W), and for the Kuskokwim and Copper River routes from about 149–164 g (Dav.) or 142 to 155 g (S&W). In all cases, the individuals would arrive without

fat reserves. Migrating Dunlins (*Calidris alpina*) and Western Sandpipers (*C. mauri*) undergo considerable fattening during spring staging on the Copper River Delta (Senner 1979). Golden-plovers also stop at this site (Isleib 1979), but details concerning possible replenishment of fat stores are lacking. It is improbable that successful trans-Pacific migration involves total depletion of fat during the spring flight. Maximizing reserves so as to buffer the unpredictable at first landfall seems the more likely strategy. To accomplish this in accordance with the flight-range formulae (see Methods), flight speed should be at or near its upper limit. We have used an estimated 104.7 km/hr (Table 4) which comes from measurements by Martin (1916) and Youngworth (1936). This figure also was applied in earlier calculations of flight ranges (Johnston and McFarlane 1967, Johnson and Morton 1976). There is no information concerning the body components of plovers at first landfall, limited data (weights of both *P. fulva* and *P. dominica*, summarized by Cramp and Simmons 1983) are available from breeding grounds. These data suggest moderate to substantial fat stores in most individuals. Studies are needed to measure fat content at landfall and to determine whether fattening typically occurs thereafter. Such knowledge would help to clarify *P. fulva*'s trans-Pacific flight speed, and might reveal that the rate employed herein should be revised downward. Given present findings (i.e., the weights of birds at or near departure as related to flight ranges and the probable need for fat at landfall in the north) we conclude that plovers ready for departure from BAFS are likely to weigh in excess of 160 g. These birds would have sufficient stores to arrive on staging areas or breeding grounds with what appear to be reasonable fat reserves (Table 4).

Johnston and McFarlane (1967) estimated that *P. fulva* use 18 g of fat in making the flight between the Aleutians and Wake Island (the distance, about 3,860 km, is the same as BAFS to the Aleutians). Based on a sample of "five plovers just arriving on Wake Island from the north" they concluded that while birds could depart from the Aleutians at a minimum weight of 143 g, it was more likely that only plovers "weighing at least 150 g attempt this 2,400-mile flight." Kinsky and Yaldwyn (1981) extrapolated from the Johnston and McFarlane fat/distance relationship, and estimated that about 40 g of fat would fuel a flight from the Pribilof Islands to Niue
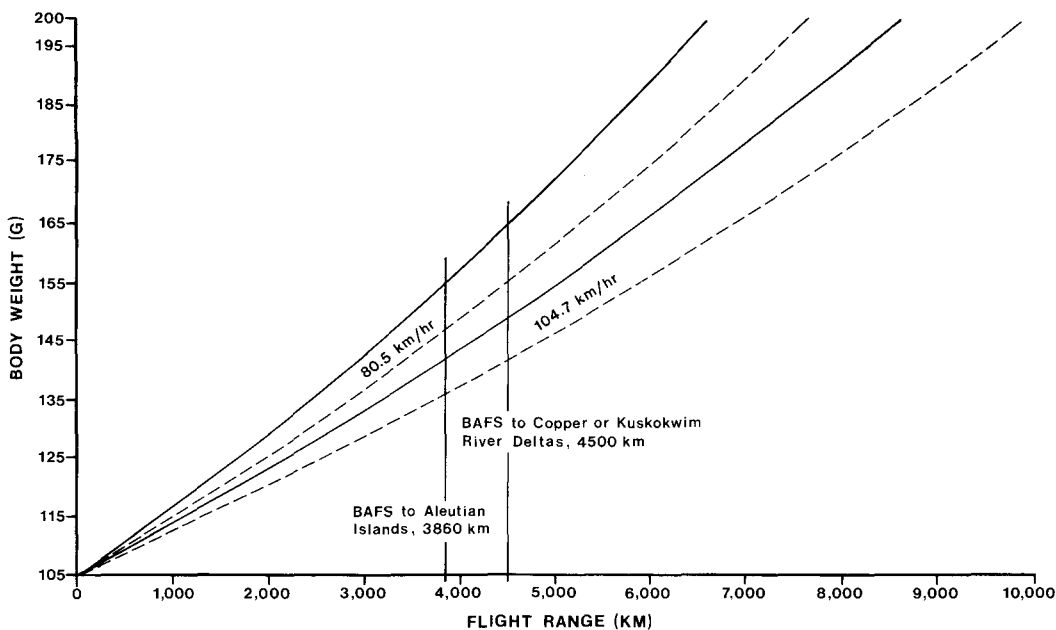
FIGURE 3. Estimated flight ranges for Pacific Golden-Plovers (assuming FFW of 105 g) according to formulae given in the text (Davidson = solid lines, Summers and Waltner = dashed lines). Possible first landfalls for northbound migrants are indicated. Some birds may fly directly to breeding grounds like the Kuskokwim Delta, (see additional comments in footnote c, Table 4). Significant numbers of *P. fulva* have never been reported in the Aleutians, and the latter may not be a major landfall for these birds. Flocks of migrant plovers have been observed in the northwestern Hawaiian Islands during early spring (Ely and Clapp 1973, Clapp and Wirtz 1975). Whether these were transients from elsewhere in the Pacific or birds that had wintered in the Hawaiian Islands is unknown. If BAFS plovers were to follow the island chain to the northwest, total flight distances would increase but the final overwater flight to the Aleutians or western Alaska would be shorter. Food resources on the small northwestern islands are probably too limited for significant replenishment of fat stores, and these sites may function mostly as brief stopovers for rest. Of the two sets of curves, 104.7 km/hr provides greater economy in use of energy reserves and possibly gives the most accurate estimates (see text). At 104.7 km/hr, flight times would be approximately 37 hr (Aleutians) to 43 hr (Copper or Kuskokwim river deltas).

Island in the southwestern Pacific, a distance of about 8,850 km. Since they found 90-g plovers at Niue in the fall, they speculated that birds weighing as little as 130 g could depart from the Pribilofs and fly nonstop to Niue Island. Based on current understanding of flight-range prediction (as embodied in the Dav. and S&W formulae), all of these investigators greatly underestimated the quantity of fat required for migration. By examining the data in Table 4, one can calculate that the fat necessary for a BAFS-Aleutians flight would range from about 37–40 g (Dav.) or 32–35 g (S&W), heavier birds using somewhat more fuel to fly a given distance than lighter ones.

In Max Thompson's fall sample of 111 adult *P. fulva* from the Pribilofs (details given earlier),

mean weight was 168.9 g (range = 120.6–251.5 g). Predicted flight ranges for these individuals (assuming 105 g FFW, and a flight speed of 104.7 km/hr) would be: 1,741–12,300 km, average 6,290 km (Dav.) or 2,031–14,098 km, average 7,280 km (S&W). It appears that the heavier birds were ready for southward departure, the status of the others (i.e., how much additional fattening occurred) is unknown. From the Pribilofs to BAFS is about 4,200 km, to Wake Island about 4,350 km. Thus, the average birds could have flown to either location, arriving there with approximately 20–27 g of reserve fat (percent unused flight range × 63.9 g of fat). These reserves are within the ranges of fat content measured in fall adults both at BAFS (Table 1) and Wake Island (Johnston and McFarlane). Some

of our birds were leaner than any taken at Wake. This probably reflects weight losses during the interval between arrival and collection (many adults were already on the BAFS area when sampling began), whereas Johnston and McFarlane may have collected their specimens at or near arrival. The leanest plovers in Thompson's sample (12 birds ranging from 120.6–138.5 g) probably accumulated additional fat prior to leaving. Without increased fuel, surviving a southward flight would have been unlikely for most of these birds since the nearest landfall (approximately 3,250 km distant in the northwestern Hawaiian Islands) exceeded their capabilities. Perhaps departure weight is of less significance if birds follow a southwestward course with stopovers (i.e., along the Aleutians to the Kurile Islands, then to Japan and the Asian coast). A golden-plover banded by Thompson on St. George Island in September and recovered 6 weeks later at Hokkaido, Japan (McClure 1974) demonstrated the possibility of such a route. Extrapolation of the curves in Figure 3 indicates that the heaviest individuals (over 210 g) captured by Thompson had very long flight ranges, and probably could have reached distant sites even beyond Niue Island without additional fattening enroute. Although radar observations from Guam suggest that *P. fulva* makes lengthy nonstop migrations across the western Pacific (Williams and Williams 1988), the maximum distances traversed by this species in continuous flight are unknown.

ACKNOWLEDGMENTS

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