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BIOLOGY OF SHOREBIRDS SUMMERING ON ENEWETAK ATOLL

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ABSTRACT—Golden Plovers, Whimbrels, Bristle-thighed Curlews, Wandering Tattlers, and Ruddy Turnstones were studied at Enewetak Atoll, Marshall Islands, during the summers of 1970 and 1973. These birds are representative of an unusual behavioral feature in shorebirds wherein many nonbreeding individuals remain on wintering areas during the boreal summer. Most appear to be first-year birds lacking the physiological stimulus for migration.

Plovers and turnstones were particularly abundant with flocks of 20 or more relatively common. Feeding activity coincided with low tides, and occurred mostly on the reef-flat along the seaward margin of the atoll. Upland sites were frequented during periods of high tide.

Testes were histologically immature except for very limited sperm production in some Whimbrels and curlews. No recrudescence of ovaries was found. Despite the lack of gonadal activity, a few individuals achieved breeding coloration. Most birds had either a partial breeding or nonbreeding plumage. The sex ratio of plovers was strongly biased toward males (about 5:1), and apparently balanced in the other species.

Golden Plovers had molted their juvenal remiges during the winter, and were well into a complete prebasic II molt by mid-July. Whimbrels and Bristle-thighed Curlews molt juvenal remiges in the spring and early summer, and were nearing completion of alternate I development in mid-July. Wandering Tattlers were replacing juvenal primaries in early summer with molt commencing from a central locus; this unusual pattern of primary molt appears to be age-related, occurring only in first-year birds. Ruddy Turnstones had no recent and/or ongoing remex molt. Evidently young birds retain juvenal wing feathers through their second summer of life. In all species studied, the development of alternate feathering was frequently very slight such that the individual would essentially pass from one basic plumage to another while on the winter range.

Fat content in summering birds varied from around 3 to 6 percent of body weight, restricting them to relatively short flights. Flight range predictions were much too conservative when calculated according to formulae based upon aerodynamic theory. Possibly the streamlined body-form of shorebirds results in greater flight efficiency than heretofore recognized in studies of avian aerodynamics.

Shorebirds display an unusual behavioral feature wherein substantial numbers of nonbreeding birds remain on wintering grounds during the boreal summer. This pattern is particularly common in long-distance transequatorial migrants. The biological basis for this phenomenon is unknown, although it appears that these are mostly first-year birds which perhaps lack the physiological stimulus or capacity for migration. Literature pertaining to migratory arrest and its possible causative factors was reviewed by McNeil (1970) and Johnson (1973).

Most of this paper will concern reproductive condition, plumage, molt, fat content, and flight range in five species of shorebirds occupying a central Pacific wintering area during midsummer. Surprisingly little is known about such features in shorebirds for this phase of their life cycles. Major portions of the material upon which this treatment is based have been published elsewhere (Johnson 1973, Johnson and Morton 1976, Johnson 1977).

MATERIALS AND METHODS

Fieldwork was conducted at Enewetak Atoll in the northwest Marshall Islands (approximately 11°N, 162°E) from 9 June through 6 July 1970; and from 4 July through 17 July 1973. The frequently used spelling "Eniwetok" represents a distortion of the native "Enewetak" which occurred during World War II and the subsequent nuclear testing period. Observations and collections were made on Aomon, Biijiri, Chinimi, Enewetak, and Rojoa islets. The following species were studied: American

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FIGURE 1. Much of the land surface at Enewetak is covered by shrubby vegetation. The predominant plants in this photograph are *Scaevola taccada* and *Ipomea tuba*.

Golden Plover (*Pluvialis dominica fulva*), Whimbrel (*Numenius phaeopus*), Bristle-thighed Curlew (*N. tahitiensis*), Wandering Tattler (*Heteroscelus incanus*), and Ruddy Turnstone (*Arenaria interpres*).

Laboratory and field techniques are detailed in other publications (Johnson 1973, Johnson and Morton 1976, Johnson 1977). Basically, procedures involved: (1) various surveys and counts of shorebirds on the atoll; (2) morphological and histological examination of gonads; (3) plumage evaluations (using flat skins) based upon fading, wear, and molt of the flight and body feathers; (4) ether extraction of lipids from preserved carcasses.

RESULTS AND DISCUSSION

THE ATOLL ENVIRONMENT

Enewetak is representative of the multitude of Micronesian atolls which collectively form an important component of wintering habitat for many shorebirds. The atoll consists of some 40 small coral islets surrounding a lagoon approximately 20 nautical miles in diameter. Substantial ecological disturbance occurred during World War II and as a result of extensive nuclear testing over the period from 1948 to 1958. Pertinent summaries of modern man's impact upon the biota of Enewetak have been published by Woodbury (1962) , Jackson (1969), and Fall et al. (1971). On many of the islets, vegetative recovery over the past two decades has produced an extensive shrub cover (mostly *Scaevola taccada* and *Messerschmidia argentea*) interspersed with open areas dominated by various grasses and forbs (Fig. 1). Present habitats are possibly more attractive to shorebirds than the more heavily vegetated predisturbance situation.

Migratory routes of shorebirds as they traverse the Pacific are not well understood. Baker (1951) postulated three major migration corridors (Fig. 2). With the exception of the Whimbrel, many of the shorebirds occurring at Enewetak probably utilize the "Nearctic-Hawaiian" route. There are only three unconfirmed

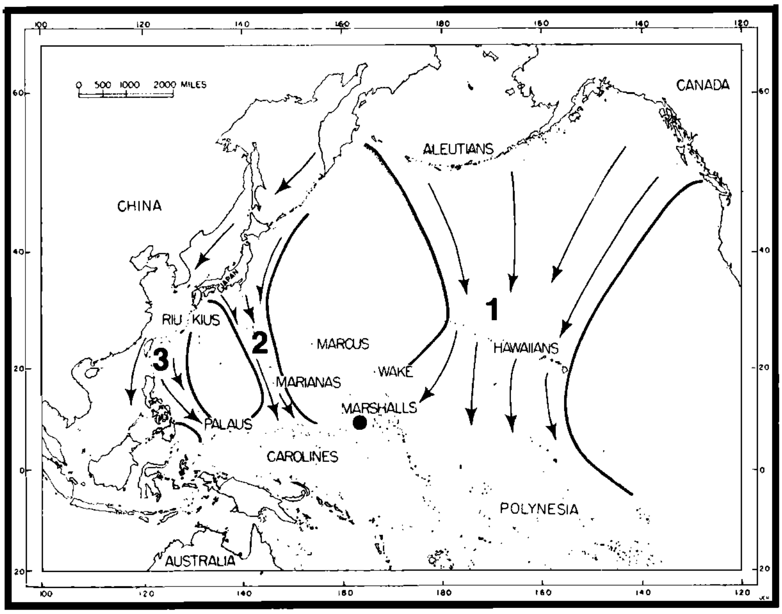

FIGURE 2. The three major migratory corridors for shorebirds in the Pacific as proposed by Baker. Corridor 1 is the "Nearctic-Hawaiian" route which probably is the most important flyway relative to Enewetak (approximate location indicated by black dot). Corridors 2 and 3 are the "Japanese-Marianan" and "Asiatic-Palauan" flyways, respectively. (From Baker 1951, with permission.)

sight records of Whimbrels in the Hawaiian area (Ely and Clapp 1973), hence their presence in Micronesia evidently occurs via eastward movements from the Asian coast and adjacent island groups (Fig. 2).

SHOREBIRD ABUNDANCE AND BEHAVIOR

Golden Plovers and Ruddy Turnstones are the most abundant shorebirds present on Enewetak during the summer with flocks of 20 or more seen commonly. Similar findings were noted by Carpenter et al. (1968) in records gathered during portions of four boreal summers spent at Enewetak. Census information is limited, and the available data are shown in Table 1. Carpenter et al. (1968) present figures for the entire atoll. However, they do not describe methods, and the accuracy of their data is difficult to assess. During my visits, it was unfeasible to survey the whole area and counting was restricted mainly to Enewetak islet.

My data in Table 1 show daily fluctuations in abundance which reflect movements of birds between adjacent islets. Plovers, for example, were sometimes absent from Enewetak islet on a given day (or portion thereof) only to reappear later. Movements appeared keyed to certain particularly desirable habitats. In 1973, an excavation (part of an ERDA project called "EXPOE") on Aomon islet produced a relatively large flat area with a freshwater pond in its center. Flocks of shorebirds congregated there (especially during periods of high tides and in the evening) with at least 100 plovers present on one occasion (Table 1). The airstrip on Enewetak islet is another attractive site, and is used extensively by plovers and turnstones. The birds loaf on the pavement, utilize freshwater puddles, and (based upon behavioral observations) appear to capture insects in grassy areas

TABLE 1
POPULATION ESTIMATES OF SUMMERING SHOREBIRDS ON ENEWETAK

Species	1966[a]	1967[a]	1970[b]	1973[b]	
Golden Plover	183	139	0–35	10–30	20–100
Whimbrel	no data	no data	0–6	1–6	0
Bristle-thighed Curlew	50	18	0–1	0	3–10
Wandering Tattler	22	24	0–12	0–4	0
Ruddy Turnstone	129	102	0–30	0–9	12–20

[a] Data for these years are from Carpenter et al. (1968), and represent total surveys of the atoll with helicopter assistance.

[b] Data for these years are those of Johnson, some of which have been published (Johnson 1973). The 1970 data represent 14 census counts on Enewetak islet only, conducted from 9 June through 6 July. Data for 1973 are respectively: first column, 5 counts on Enewetak islet from 4 July through 17 July; second column, 2 counts on Aomon islet, 10 and 15 July. Values of "0" represent daily fluctuations at a particular site, and reflect intra-atoll movements of birds.

along the runway aprons. Intra-atoll movements of highly mobile shorebirds make it very difficult to obtain accurate estimates of total populations. My observations on only two islets of the forty making up the atoll would imply that the Carpenter et al. (1968) figures are too conservative. On the other hand, habitat conditions on the islets which I surveyed perhaps attracted disproportionately large numbers of birds; also population levels might fluctuate from one year to another.

During periods of low tide, birds leave upland sites and feed in the intertidal zone. Feeding was confined almost exclusively to the seaward margin of the atoll with birds seen only infrequently on the lagoon side. An extensive and productive reef-flat community (Odum and Odum 1955) accounts for the attractiveness of the seaward zone to feeding shorebirds (Fig. 3). In contrast to plovers and turnstones which commonly frequented upland sites, Whimbrels, curlews, and tattlers behaved differently. The latter species were encountered almost exclusively on beach and intertidal habitats. Bristle-thighed Curlews were infrequent on Enewetak islet, but relatively common on various of the other islets. Possibly, this species is particularly intolerant of human activity (which is substantial on Enewetak islet) and prefers relatively undisturbed sites.

SEX RATIOS AND REPRODUCTIVE CONDITION

Van Oordt (1928) found that summering populations of Knots (*Calidris canutus*) and Ruddy Turnstones in Holland contained a preponderance of males. A similar disparity occurs at Enewetak, but thus far it is apparent only among Golden Plovers. The combined tally by species and sex for all birds collected in 1970 and 1973 is: Golden Plover, 25 males and 6 females; Whimbrel, 2 males and 4 females; Bristle-thighed Curlew, 3 males and 5 females; Wandering Tattler, 4 males and 7 females; Ruddy Turnstone, 13 males and 9 females. It is reasonable to assume that the foregoing reflects random sampling since birds were collected opportunistically. The significance of the distorted sex ratio in plovers is unknown. Perhaps females are more likely to achieve sexual maturity and return to breeding areas in their first year, or possibly there is differential movement of the two sexes on the wintering grounds resulting in geographic separation.

In almost all males, the testes were small and inactive. No sperm were being produced in any of the plovers, tattlers, or turnstones collected (Table 2). In one of two Whimbrels, and one of three curlews examined, testicular development had proceeded to the extent that a few spermatozoa were present. It is doubtful

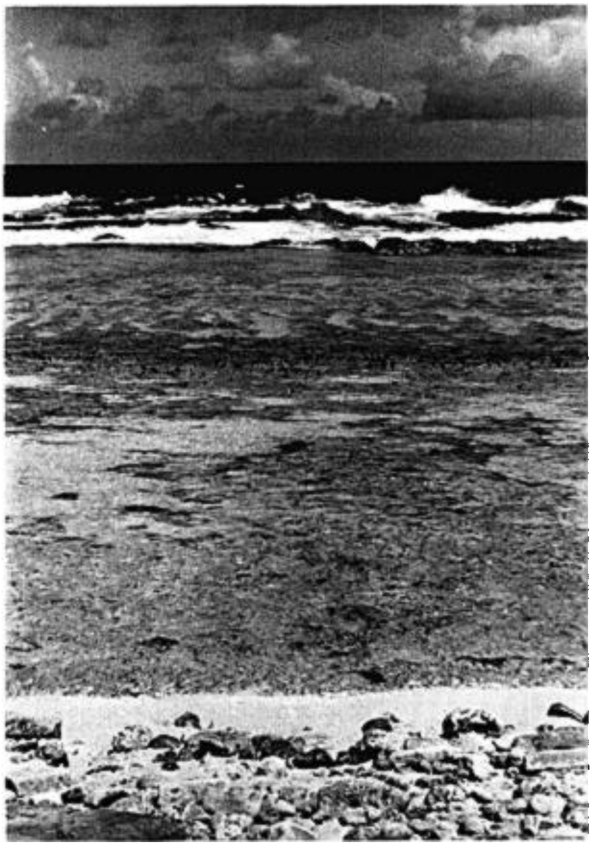

FIGURE 3. A biologically diverse and productive reef-flat occurs along the seaward margin at Enewetak. In some areas it is much wider than in this photograph. Shorebirds fed extensively on such habitat during low tides.

TABLE 2

SUMMARY OF REPRODUCTIVE ORGAN DEVELOPMENT[a]

Species (N)	Range in wt. both testes (mg)	Sperm production	Range in ovary wt. (mg)	Range in dia. largest follicles (mm)	Egg production	Range in oviduct wt. (mg)
Golden Plover (23♂, 6♀)	5–40	no	29–80	1.4–2.0	no	13–71
Whimbrel (2♂, 3♀)	23–45	limited	63–102	1.3–1.5	no	66–77
Bristle-thighed Curlew (3♂, 5♀)	10–63	limited	45–66	1.1–1.4	no	71–111
Wandering Tattler (2♂, 6♀)	4–6	no	33–79	0.9–1.8	no	13–38
Ruddy Turnstone (11♂, 7♀)	2–27	no	22–64	1.1–1.6	no	16–19

[a] The table is a composite of both published (Johnson 1973) and unpublished data.

FIGURE 4. Variations in the plumage of Golden Plovers summering on Enewetak. The bird on the left showed partial alternate development with scattered black feathers on the cheeks, throat, and breast; plus a fairly distinct white stripe over the eye and down the side of the neck. The other specimen displayed alternate feathering. (From Johnson 1973.)

that either individual would have been fertile since sperm production was very low. The ultimate degree of testicular recrudescence among summering shorebirds is unknown; however, based upon collection dates (early to midsummer) further maturation seems unlikely. Additional details on testicular histology are given elsewhere (Johnson 1973).

Although van Oordt (1928, 1931) postulated a direct relationship between extent of development of the testes and type of plumage in summering shorebirds, my data do not fully support this correlation. Variations occurred in testis weight (Table 2), with larger testes displaying at least partial activation of the seminif-

TABLE 3
SUMMARY OF PLUMAGE AND MOLT[a]

Species	Remiges	Rectrices	Body molt	Overall appearance[b]
Golden Plover	Vary from unworn to moderately worn basic I feathers; prebasic II molting through primary 6 in some birds; secondary molt commences with loss of primary 6.	Replaced in most birds during prebasic I molt; molting commences with loss of primary 5 or 6.	Extensive in most birds.	A, P, B; undergoing prebasic II molt.
Whimbrel and Bristle-thighed Curlew	Prebasic I molt recently completed or nearing completion.	Erratic pattern of prebasic I molting, some juvenal feathers retained; no molt occurring.	Slight	P, B
Wandering Tattler	Prebasic I molt underway; unusual pattern of primary loss commencing of a central locus.	Erratic pattern of prebasic I molting, molt underway in 2 of 3 specimens.	Slight	B
Ruddy Turnstone	Basic I in probable 2nd-year birds, juvenal in 1st-year birds; no molt occurring in either group.	As with rectrices	Slight	A, P, B

[a] Data from Johnson (1977) represent birds collected during the period from 4 through 17 July 1973.

[b] A = alternate (bright reproductive coloration); P = partial alternate (moderate reproductive coloration); B = basic (no reproductive coloration). The variation reflects individual differences in the extent to which alternate body feathering is acquired in the late winter and spring. Birds considered "basic" have so few alternate feathers that they essentially molt from one basic plumage to another.

erous epithelium (i.e. increased numbers of primary spermatocytes in synapsis). This modest recrudescence implies elevated levels of gonadotropins in the blood, and perhaps also the secretion of testicular androgens. Nonetheless, birds with larger testes were often in a drab nonbreeding plumage.

All females collected at Enewetak had small and inactive reproductive organs (Table 2). Similar findings were reported in several species of summering shorebirds by van Oordt (1928, 1931) and Loftin (1962). Further information on my specimens is available elsewhere (Johnson 1973).

PLUMAGE AND MOLT

General features of plumage development in each species are summarized in Table 3. A more detailed treatment was published by Johnson (1977), and only major findings will be discussed in this paper.

The plumage of each individual was a composite of old and new feather generations, with the result that birds varied conspicuously in appearance. Some had predominantly new plumage with resultant bright coloration and vice versa (Figs. 4, 5). In many birds, the development of alternate feathering is so slight that the

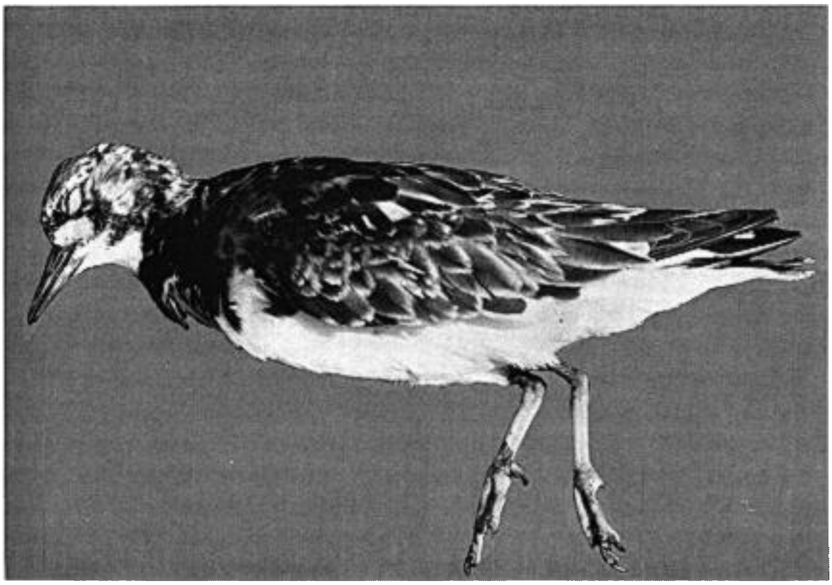

FIGURE 5. Partial alternate feathering was relatively common among Ruddy Turnstones at Enewetak. Such individuals had scattered chestnut-colored feathers dorsally, and a faint harlequin face pattern. (From Johnson 1973.)

individuals essentially remain in basic plumage during the summer period. At Enewetak, basic and partial alternate plumages are much more common than alternate in flocks of summering birds. Golden Plovers were particularly easy to observe, and our counts of various flocks (generally 20–30 birds per flock) indicated alternate plumage in only about 10 percent of the individuals seen.

The remainder of this section will describe pertinent findings in each of the species studied.

Golden Plovers varied in relative wear of flight feathers. In some, the primaries were bright brown-black in color and unworn; in others, there was moderate fading and wear (Fig. 6). If some first-year birds molt their primaries during the winter and others do not, then moderately worn feathers should represent the juvenal plumage. However, these feathers were not nearly so worn as definite juvenal primaries in the other species studied (Fig. 7). Hence, it appears that all first-year plovers replace their juvenal remiges when they molt into basic I plumage during the winter. The degree of wear would then relate to at least two factors—the chronology of molting and the extent to which birds move on the winter range subsequent to molt. Substantial individual variation as to the onset and rate of primary molt has been described in Golden Plovers and other shorebirds (Middlemiss 1961, Johnston and McFarlane 1967, Thomas and Dartnall 1971a, b, Pearson 1974, Dare and Mercer 1974, Evans 1975, Elliott et al. 1976). It is likely that the Golden Plover population at Enewetak in early summer represents a composite with some birds perhaps resident since fall migration and others arriving after flying varying distances during the winter and spring. Differences in primary wear would thus be an interaction between two variables—when the feathers were acquired and the subsequent mileage placed upon them.

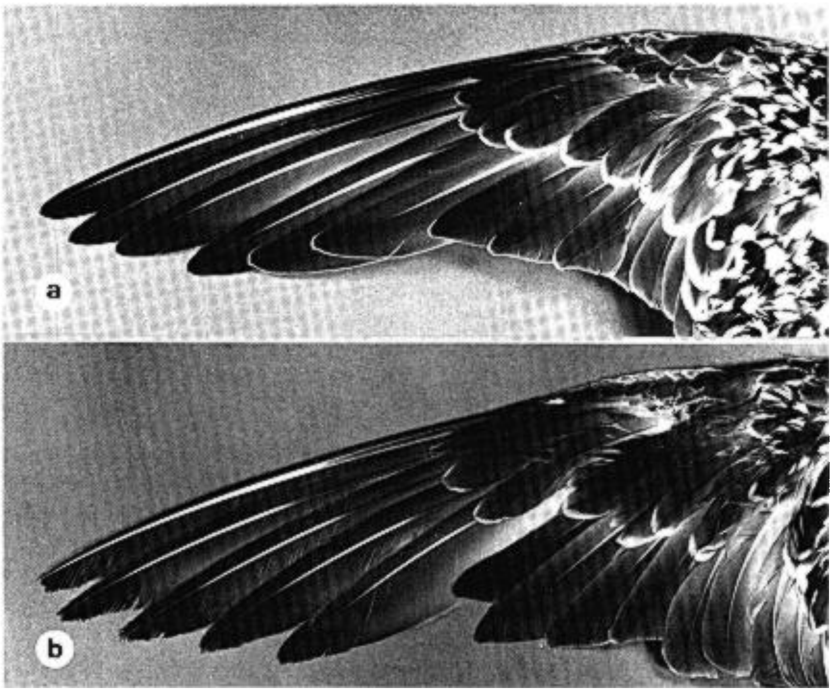

FIGURE 6. Wings from Golden Plovers collected in early July at Enewetak. (a) Primaries 1–4 are new (4 is short and hidden from view); primaries 5–10 represent an unfaded and unworn feather generation that is being replaced. (b) Primaries 1–5 are new (5 is short and hidden from view); primaries 6–10 are moderately worn and faded, but not to the degree characteristic of juvenal feathers. Hence, the same feather generation is being replaced in each specimen. The wings shown represent the extremes in the range from unworn to moderately worn primaries. All other plovers examined fell within the limits illustrated here. (From Johnson 1977.)

Plovers throughout the gradient of feather wear (Fig. 6) were molting their primaries. Some had progressed as far as primary 6. There was also extensive body molt in progress, hence the birds were undergoing a complete prebasic II molt in early summer. This appears to be out of synchrony with the molt schedule of plovers on the northern breeding grounds.

Whimbrels and Bristle-thighed Curlews molt their juvenal primaries in the spring to early summer period. Most of the birds examined had completed wing molt; two individuals were still molting extremely worn juvenal primaries when collected on 6 and 15 July 1973, respectively. In contrast to the plovers, these species would have a later prebasic II body molt which may in fact be chronologically similar to corresponding prebasic molting in postnuptial adults. Body molt was slight, and the birds were nearing completion of alternate I plumage development. The latter varies among individuals as to the number of more brightly colored alternate feathers in the overall plumage (Table 3).

Wandering Tattlers were molting juvenal remiges in July. The pattern of primary molt is unusual in that it commences centrally with primary 6, then proceeds distally to primary 10 (Fig. 7). Following the loss of primary 10, my small sample of specimens molted sequentially primaries 1, 5, and 4; I was unable to trace

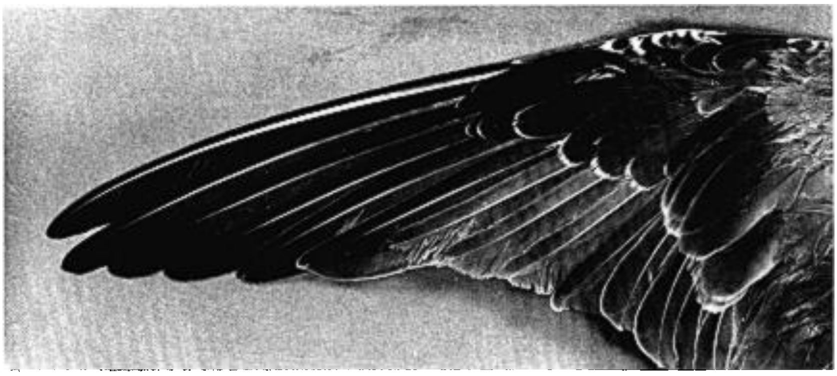

FIGURE 7. Wing from a Wandering Tattler collected in mid-July at Enewetak. Primaries 2, 3, and 4 are worn, faded juvenal feathers which typify the appearance of similar feathers in Whimbrels, curlews, and turnstones. The pattern of primary replacement is unusual in tattlers since it commences with feather 6. (From Johnson 1977.)

events further with the materials available. In contrast to the above, museum skins of Wandering Tattlers often show the typical shorebird sequential molt pattern commencing with primary 1. Comparable findings were reported in Wandering Tattlers and Polynesian Tattlers (*Heteroscelus brevipes*) by Prater and Marchant (1975), and in several other species of shorebirds by Pearson (1974) and Elliott et al. (1976). Each of these investigators concluded that the variation is age-related with central locus molting restricted to first-year birds.

Tattlers had fewer alternate feathers than any of the other species examined (Table 3). Hence, the alternate I condition in these birds involves a very drab plumage consisting mainly of worn basic feathers and probably some juvenal feathers as well.

Ruddy Turnstone specimens were divisible into definite first-year and probable second-year age-groups (see Acknowledgments). First-year birds had retained their juvenal remiges, while in second-year birds these feathers were referable to the basic I plumage. Neither group showed any recent and/or ongoing remex molt. Evidently, first-year birds utilize juvenal wing feathers through their second summer of life. This pattern is comparable to those shorebirds which are short-distance migrants, and which typically replace their juvenal remiges during the prebasic II molt (Witherby et al. 1940, Palmer 1967, Pearson 1974). The data suggest that the timing of subsequent prebasic molt in summering turnstones might coincide with that of postnuptial adults.

Overall feathering in turnstones (Table 3) was distributed as follows relative to the two age-groups: first-year, 2 partial alternate and 1 basic; second-year, 2 partial alternate and 1 alternate.

FAT AND FLIGHT RANGE

Fat cyclicity has not been examined widely in shorebirds. The primary studies are those of Johnston and McFarlane (1967) on Golden Plovers at Wake Island in the Pacific; McNeil (1969, 1970) and McNeil and Cadieux (1972a, b) on various charadriids and scolopacids in the Gulf of St. Lawrence and in northeastern Venezuela; Page and Middleton (1972) on Semipalmated Sandpipers (*Ereunetes*

TABLE 4

FAT CONTENT OF SUMMERING SHOREBIRDS[a]

Species (N)	Body wt. (g)[b]	Ether-extractable fat (g)[b]	Fat content as % of body wt.[b]
Golden Plover (17)	116.9 (102.5–129.8)	3.4 (1.9– 5.5)	3.0 (1.7– 4.6)
Whimbrel (2)	401.2 (384.5–418.0)	23.9 (22.1–25.8)	6.0 (5.3– 6.7)
Bristle-thighed Curlew (7)	493.9 (383.0–585.0)	33.6 (12.7–63.1)	6.6 (3.3–10.8)
Wandering Tattler (3)	115.8 (96.5–132.5)	3.6 (2.5– 4.3)	3.0 (2.6– 3.6)
Ruddy Turnstone (6)	97.1 (89.1–108.0)	3.9 (2.8– 4.7)	4.0 (2.9– 4.7)

[a] Data from Johnson and Morton (1976) represent birds collected during the period from 4 through 17 July 1973.

[b] Figures represent mean and range.

pusillus) at Long Point, Ontario; and Baker (1975) on Pied Oystercatchers (*Haematopus ostralegus finschi*) in New Zealand. Only the Venezuela research provides substantial data for birds summering on their wintering grounds. To my knowledge, the information presented below (and in part elsewhere, Johnson and Morton 1976) is the first consideration of lipids in shorebirds summering on a Pacific winter range.

The data are summarized in Table 4. Fat levels varied from 3.0 to 6.6 percent of body weight. In contrast, premigratory or intramigratory fat in shorebirds ranges from around 17 to 50 percent of body weight (Johnston and McFarlane 1967, McNeil 1970, Page and Middleton 1972). The slightly higher levels of fat in Whimbrels and curlews (Table 4) may relate to their molt status (nearing completion of prealternate molt), as described earlier.

Flight range estimates for the species examined are given in Table 5. The data shown represent the leanest compared to the fattest bird in each species. Calculations appearing in the first column of range estimates ("A" in Table 5) interrelate speed of flight and energy stores to the rate of energy use during flight. Such estimates are inherently crude since flight speed is essentially a "guess" and other variables (effects of wind, etc.) cannot be delimited. Presumably, relatively fat Whimbrels and curlews were capable of sustained flights of about 600 to 800 miles with flight ranges in the other species substantially less (Table 5).

TABLE 5

APPROXIMATE CAPACITY FOR SUSTAINED FLIGHT

Species	Body wt. (g) and ether-extractable fat (g)[a]	Flight speed (mph)[b]	Flight range (miles)[c]	
			A	B
Golden Plover	108.8 (1.9), 119.5 (5.5)	65	160–430	80–200
Whimbrel	418.0 (22.1), 384.5 (25.8)	45	470–590	190–260
Bristle-thighed Curlew	383.0 (12.7), 585.0 (63.1)	35	225–820	125–455
Wandering Tattler	96.5 (2.5), 118.5 (4.3)	45	160–235	100–150
Ruddy Turnstone	97.5 (2.8), 90.0 (4.2)	40	155–250	120–200

[a] Data from Johnson and Morton (1976) represent birds collected during the period from 4 through 17 July 1973. For each species, the figures show the two specimens with minimum-maximum flight ranges, respectively.

[b] Flight speed estimates from several sources where literature summaries of such data and/or direct speed measurements are given: Cooke (1933), Meinertzhagen (1955), Johnston and McFarlane (1967), McNeil (1970).

[c] For column A, the formula used by McNeil (1969, 1970), McNeil and Cadieux (1972 a, b) and Baker (1975) was used to calculate flight range: FR = flight range in miles = $F \times S \times 9.1$ kcal/FM; where F is weight of fat in grams; S is flight speed in miles per hour; 9.1 is the caloric value of 1 gram of fat (Johnston 1970); and FM is flight metabolism. The latter is estimated by the equation of Raveling and LeFebvre (1967): $\log FM = \log 37.152 + 0.744 \log W \pm 0.074$, where W is body weight in kilograms.

For column B, the formulae and tables given by Pennycuick (1975, pp. 25–28) were used in the calculations.

All birds would have been restricted to "island-hopping" in Micronesia with no physiological potential for long-distance migration.

Range estimates in the second column ("B" in Table 5) are calculations derived from Pennycuick's (1975) formulae. The latter rest upon aerodynamic principles which avoid the questionable variables mentioned above. Results indicate considerable disagreement between the two approaches with the Pennycuick approach predicting shorter flight ranges (Table 5).

The discrepancy was greater than anticipated, and as a further test I applied both methods to data on Golden Plovers provided by Johnston and McFarlane (1967). One can select values from their paper representative of fat content in birds about to depart Wake Island northbound for the Aleutians. Here we have a known event about to occur—namely a 2400-mile flight, and the necessary variables to fit the formulae. Assuming that the fattest birds collected by Johnston and McFarlane were ready to migrate and that all fat would be burned as fuel, formula "A" predicts flight ranges of about 2800–4650 miles and formula "B" about 1250–2100 miles. It is most unlikely that all fat would be utilized during the flight. In fact, Johnston and McFarlane found that southbound plovers still contained substantial stores of lipids upon arrival at Wake Island in August.

Since formula "B" predicts that the birds would fail to reach the Aleutians, Pennycuick's approach as applied in this particular instance is much too conservative. The application of aeronautical concepts to birds obviously needs refinement, and my purpose in reporting these findings is cautionary rather than critical. Pennycuick (pers. comm.) feels that body shape and its relationship to surface drag may explain the discrepancy between actual and predicted flight range in Golden Plovers. The extent to which notable avian streamlining (as in shorebirds) reduces drag has not been studied adequately. In any event, shorebird flight appears to be highly efficient and at variance with present concepts of avian aerodynamics.

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