PLUMAGE AND MOLT IN SHOREBIRDS SUMMERING AT ENEWETAK ATOLL

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ABSTRACT.—Various features of plumage and molt were studied in Golden Plovers, Whimbrels, Bristle-thighed Curlews, Wandering Tattlers, and Ruddy Turnstones. Specimens collected during July 1973 at Enewetak Atoll, Marshall Islands, represent birds that had not migrated to the northern breeding grounds. Based upon several criteria (bursa of Fabricius, wear of remiges and rectrices, and the condition of body feathers) most specimens appeared to be first-year birds. The relative development of alternate plumage showed considerable individual variation, which presumably reflects physiological variability in the factors controlling prealternate molt in the late winter and spring. Many birds remain in nonbreeding plumage (exhibiting only a few alternate feathers), and essentially pass from one basic plumage to another while on the winter range. Plovers replace primaries, secondaries, and some tertials during the winter, and were undergoing a complete prebasic molt in July. Such a pattern varies considerably from molt chronology in postnuptial adults. Whimbrels and Bristle-thighed Curlews finish wing molt in the late spring to midsummer, and birds collected in July had not yet begun prebasic molt. Wandering Tattlers were molting juvenal remiges commencing with the 6th and progressing to the 10th primary. The molting sequence of primaries 1 through 5 was not entirely clear. Museum skins indicated that remige molt starts with the 1st primary in some specimens. The overall pattern awaits detailed study for clarification. No indications of prebasic molt were found in summering turnstones, hence subsequent timing of this molt may coincide with that of postnuptial adults. As no wing molt was occurring, first-year birds apparently retain their juvenal remiges until the prebasic II molt. In each species, summering birds showed considerable individual variability in ongoing rectrix molt. Also some specimens had replaced a few or all of these feathers during the preceding winter while others had not.—*Department of Biology, Moorhead State University, Moorhead, Minnesota 56560.* Accepted 6 August 1975.

MANY shorebirds, particularly the long-distance migrants, remain on their wintering grounds during the boreal summer. Presumably this nonbreeding contingent is composed primarily of first-year birds. Literature pertaining to migratory arrest and its possible causative factors was reviewed by McNeil (1970) and Johnson (1973). Plumage data for shorebirds summering on winter ranges are scattered and fragmentary, and altogether relatively little is known. To my knowledge there are no detailed reports representing the summer period in the Pacific. This paper describes plumage and molt in five species of shorebirds collected on a central Pacific wintering ground during midsummer.

MATERIALS AND METHODS

Fieldwork was carried out at Enewetak (formerly spelled Eniwetok) Atoll in the northwest Marshall Islands (approximately 11°N, 162°E) from 4 through 17 July 1973. Birds were collected on Aomon, Biijiri, Enewetak, and Rojoa islets. The species studied are listed in Table 1.

Plumage was evaluated (using flat skins) according to four criteria: (1) Degree of wear and fading of color in the remiges and rectrices. (2) Ongoing molt of the flight feathers. (3) Degree of body molt (nonflight feathers) as evidenced by relative activity of feather papillae viewed on the inner surface of the skin. Particular emphasis was given to the capital, spinal, and femoral pterylae. Specimens were ranked "S" if only scattered feather growth was noted, or "G" if a moderate to heavy general molt was occurring. (4) Each bird was assigned to one of three categories descriptive of overall feathering: Basic, partial alternate, and alternate. Basic represents feathering made up almost entirely of very worn and faded elements; partial alternate reflects a mixture of old and new producing moderate reproductive coloration; alternate indicates that most feathers were newly acquired and the specimen was brightly colored.

Each species examined had 11 pairs of primary remiges and 6 pairs of rectrices. The vestigial 11th

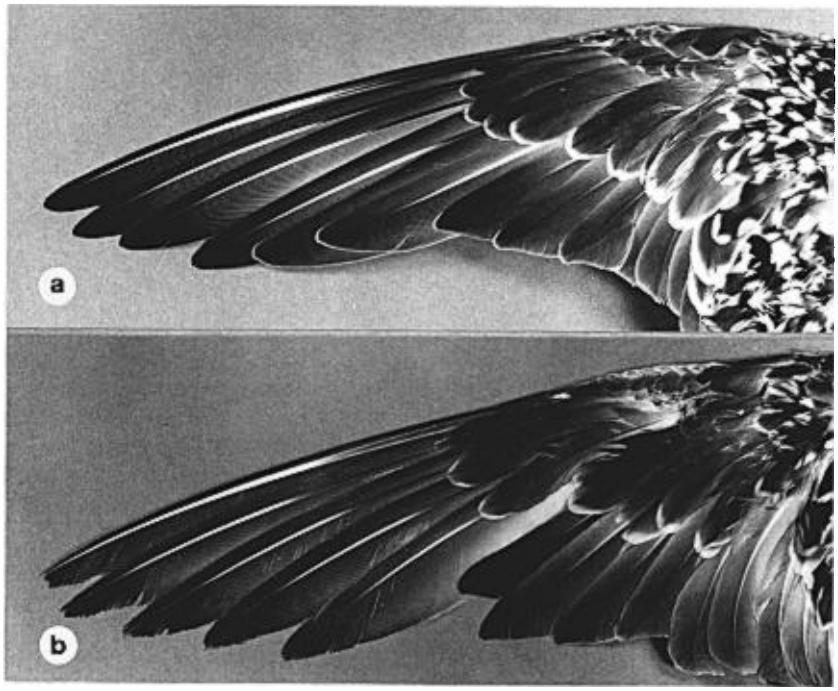

Fig. 1. Wings of Golden Plovers with primary molt underway. (a) Plover No. 12 where primaries 1–4 are new (4 is very short and hidden from view). Primaries 5–10 represent an unfaded and unworn feather generation that is being replaced. (b) Plover No. 15 where primaries 1–5 are new (5 is short and hidden). Primaries 6–10 are moderately worn and faded, but not nearly to the extent characteristic of juvenal feathers. Hence the generation being replaced is the same in each bird (see text). The specimens shown represent the extremes in the range from unworn to moderately worn primaries (Table 1). All other plovers fell within the limits illustrated here.

primary (Witherby et al. 1940) was ignored, and only features pertaining to the 10 large primaries are described. The primary numbering sequence used herein is a progression where #1 represents the most proximal feather. The central rectrices were considered as pair No. 1 with the sequence progressing bilaterally.

Results

Prior to specific descriptions, which are concerned mainly with flight feathers, certain generalities pertain to all birds collected. Plumages were a composite of old and new generations. Some birds had predominantly new plumage with resultant bright coloration, and vice versa. Only two specimens were in full alternate plumage, all others varied from partial alternate to basic (Table 1). When evaluating the appearance of overall feathering, it was particularly helpful to assess the condition of back feathers, scapulars, and median and lesser secondary coverts. In alternate birds, these feathers were mostly unworn and bright. In partial alternate and basic birds, new back-scapular feathers were either moderately abundant or very few, respectively; secondary coverts were mostly old and worn in both plumages.

A general molt of body feathers was occurring in most plovers; whereas only scattered body molt was found in all Whimbrels, curlews, and turnstones, and in two of the three tattlers (Table 1). Birds undergoing light molt showed feather growth mainly in the capital and spinal tracts.

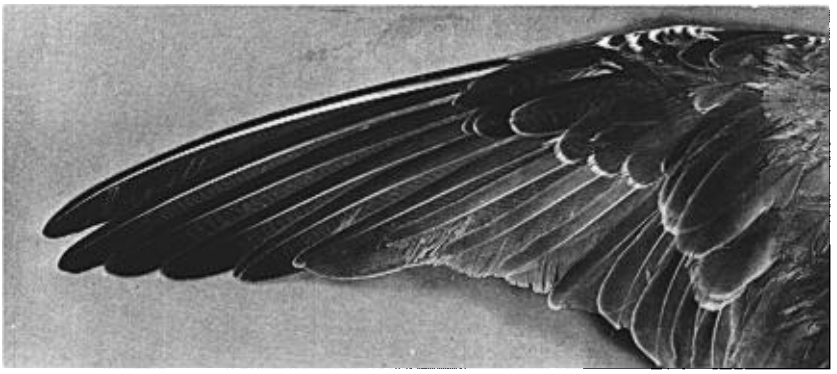

Fig. 2. Wing from Wandering Tattler 3. Primaries 2, 3, and 4 are very worn and faded juvenal feathers; all other primaries are new. The pattern of primary replacement is unusual and commences with feather 6 (see text). The juvenal primaries seen here typify the appearance of similar feathers in Whimbrels, curlews, and turnstones.

Golden Plover.—Based upon the condition of primaries, each specimen fell into one of three groups: (1) Primaries showing no wear, bright brown-black in color (Fig. 1a), one bird with no primary molt occurring, two with primary molt underway (specimens 1, 11, and 12, respectively, Table 1). (2) Primaries slightly worn and faded at the tips, some birds were not molting primaries, others were (specimens 2 and 3, 4–10, respectively, Table 1). (3) Tips and edges of primaries moderately worn and faded (Fig. 1b), all birds in primary molt (specimens 13–17, Table 1). The tertials in each of the three groups were a mixture of worn, faded feathers plus brighter more recently acquired plumage. Brightly colored tertials were more abundant in birds from groups 1 and 2 as compared to group 3 specimens.

The loss of flight feathers begins with the innermost primary (No. 1). During the collection period, individual progression into wing molt varied from primaries 1 through 6 (Table 1). The greater primary coverts are molted at approximately the same time as their corresponding primaries. Initial molt of the secondaries coincided with the loss of primary 6 (Table 1) and involved the most distal secondary. Present materials were sufficient to demonstrate only the onset of secondary replacement. No molt of tertial feathers was seen.

The beginning of rectrix molt apparently coincides with the loss of primary 5 or 6 (Table 1). Whether the central pair or pair 2 is first to be molted appears variable. Only three specimens were molting rectrices when collected. Two of these had unworn central feathers with pair 2 growing (bases of feathers scaled). In the other bird the central pair was worn and pair 2 newly replaced.

Whimbrel and Bristle-thighed Curlew.—Two patterns of plumage and associated molt typified both species: (1) One of the two Whimbrels (No. 1, Table 1), and most curlews (Nos. 1–6, Table 1) showed unworn primaries and secondaries that had been recently acquired. Their rectrices exhibited slight wear, and no molt of flight feathers was occurring. (2) Primaries, secondaries, and tertials in Whimbrel 2 and curlew 7 were extremely worn and faded. Primary molt was underway with feathers 1–4 and 1–5 newly acquired in the Whimbrel and curlew, respectively (Table 1). Wing molt begins with primary 1, and greater primary coverts are renewed consecutively with their respective primaries. No molt of secondaries, tertials, or rectrices was found. The rectrices in Whimbrel 2 (especially the central pair) were very worn. Those in

TABLE 1
PLUMAGE AND MOLT RECORDS

Spec. No.	Sex	Bursa weight (mg)[1]	Overall feathering	Remige and rectrix molt[2]	Body molt[3]	Date collected (1973)
American Golden Plover (*Pluvialis dominica fulva*)						
1	Male	—	Partial	u0, a, a	S	12 July
2	Male	—	Alternate	s0, a, a	G	8 July
3	Female	—	Partial	s0, a, a	G	10 July
4	Female	—	Basic	s1, a, a	G	6 July
5	Male	5	Partial	s1, a, a	G	6 July
6	Male	8	Partial	s1, a, a	S	10 July
7	Male	—	Partial	s2, a, a	S	10 July
8	Female	27	Partial	s2, a, a	G	12 July
9	Male	2	Basic	s2, a, a	S	9 July
10	Female	70	Basic	s3, a, a	G	12 July
11	Male	—	Partial	u3, a, a	G	10 July
12	Male	—	Partial	u4, a, a	G	9 July
13	Male	103	Partial	m4, a, a	G	6 July
14	Male	—	Partial	m4, a, a	S	8 July
15	Male	6	Basic	m5, a, x	G	7 July
16	Male	71	Basic	m6, x, x	G	12 July
17	Male	—	Basic	m6, x, x	G	12 July
Whimbrel (*Numenius phaeopus*)						
1	Female	472	Basic	u0, a, a	S	6 July
2	Female	583	Basic	w4, a, a	S	6 July
Bristle-thighed Curlew (*Numenius tahitiensis*)						
1	Female	446	Partial	u0, a, a	S	10 July
2	Male	—	Partial	u0, a, a	S	10 July
3	Female	556	Partial	u0, a, a	S	15 July
4	Female	96	Basic	u0, a, a	S	15 July
5	Female	409	Basic	u0, a, a	S	15 July
6	Female	213	Basic	u0, a, a	S	15 July
7	Male	465	Basic	w5, a, a	S	15 July
Wandering Tattler (*Heteroscelus incanus*)						
1	Male	124	Basic	w10[4], x, x	S	7 July
2	Female	35	Basic	w10, x, a	S	7 July
3	Female	201	Basic	w10, 5, 4; x, x	G	13 July
Ruddy Turnstone (*Arenaria interpres*)						
1	Male	9	Alternate	s0, a, a	S	6 July
2	Male	21	Partial	s0, a, a	S	10 July
3	Male	10	Partial	s0, a, a	S	15 July
4	Female	71	Partial	w0, a, a	S	6 July
5	Male	100	Partial	w0, a, a	S	10 July
6	Female	70	Basic	w0, a, a	S	6 July

[1] Dash indicates that no bursa was present.
[2] Sequence of letters and numbers refers to primaries, secondaries, and rectrices, respectively. Relative to primaries, the symbol u indicates unfaded and unworn, s denotes slight wear at feather tips, m indicates moderate wear, w designates extremely worn and faded juvenal feathers; 0 indicates that no molt was occurring; where molt was underway, the number shows the most recently acquired new primary. Relative to secondaries and rectrices, a denotes absence of molt while x indicates molt (see text for details).
[3] Scattered molt of body feathers denoted by S; moderate to heavy general body molt indicated by G.
[4] Wandering Tattlers have an unusual pattern of primary molt (see text).

curlew 7 showed an erratic pattern of wear—one 6th rectrix was only slightly worn with the contralateral feather extremely worn, and the central pair of feathers was less abraded than the others.

The tertials in both groups were a composite of old and new feathers. Compared to the other remiges, tertial wear was more extensive. Possibly this is due to the long, slender shape of these feathers, which might form a substantial trailing edge during flight.

Wandering Tattler.—An unusual pattern of primary molt was demonstrated wherein primary 1 is not dropped first. In specimens 1 and 2 (Table 1) primaries 1–5 were very worn and faded while 6–10 were new (Nos. 9 and 10 still partly sheathed

and growing). Wing molt in specimen 3 was more advanced, the only worn primaries being 2 and 3 in the right wing and 2, 3, and 4 in the left (Fig. 2). All other primaries were new with scaled bases restricted to 4 and 10 on the right, 5 and 10 on the left (Table 1). Worn greater primary coverts were often associated with new primaries, hence their replacement was not well correlated with primary molt.

Secondary molt begins with the outermost feather, and apparently commences at about the time primary 10 is shed or perhaps earlier in some birds. Specimen 3, for example, had replaced all secondaries (the innermost two were partly sheathed and growing) with several worn primaries still in place as described above. Tertial molt was not found in any of the specimens.

Rectrix molt was highly variable. Specimen 2 displayed worn rectrices with no molt occurring. In tattler 1, pairs 1 and 2 were relatively new and unscaled; pair 3 was partly sheathed and growing; pairs 4, 5, and 6 were faded and very worn. This implied a centrifugal pattern commencing with the central pair. However, such regularity was not found in specimen 3 where pairs 1 and 5 were scaled and growing; 3, 4, and 6 were new but unscaled; and 2 was old and very worn.

Ruddy Turnstone.—No remige or rectrix molt was found in any of the six specimens collected. Three birds (Nos. 1–3, Table 1) had unfaded primaries, secondaries, and rectrices, all of which showed only slight wear. The others (Nos. 4–6, Table 1) displayed worn and frayed remiges and variation with respect to rectrices. In specimens 4 and 6 the latter were very worn, while in No. 5 the rectrices were relatively fresh. Tertials were a mixture of old and new in all birds examined, with a preponderance of newer feathers in the more brightly colored individuals.

DISCUSSION

Various features of shorebird plumages and molts are described in the major works by Bent (1929), Witherby et al. (1940), and Palmer (1967). From these sources, and also from other studies (Middlemiss 1961; Holmes 1966; Stresemann and Stresemann 1966; Johnston and McFarlane 1967; Thomas and Dartnall 1971a, 1971b; Thomas 1972; Burger and Howe 1975), several concepts emerge that are applicable to the long-distance migrants found at Enewetak: (1) Postnuptial birds undergo prebasic body molt partly on the breeding grounds and partly during southward migration over a period from late summer to late fall. Molt of flight feathers is generally delayed until migration is completed, and thus occurs through the winter months. (2) Adult prealternate molt (body feathers only) takes place on the wintering grounds in the late winter and spring. (3) Molt (into basic I) of individuals in their first winter involves body feathers, remiges, and often some rectrices. The generalization that juvenal wing feathers are retained until the prebasic II molt (Witherby et al. 1940; Palmer 1967) is incorrect in the case of shorebirds that migrate over great distances (Stresemann 1963). Among these highly mobile forms, Stresemann and Stresemann (1966) found that some species renew wing feathers in their first winter and migrate north in the spring, while other species remain in southern regions during the boreal summer and begin wing molt at from 5 to 12 months of age. (4) Prealternate molt of first-year birds begins in late winter resulting in the replacement of body feathers to varying degrees.

As stressed by Loftin (1962) and McNeil (1970), the correct identification of first-year birds is inherently difficult. There is no precise information on atrophy of the bursa of Fabricius in shorebirds. McNeil and Burton (1972) claimed that the organ

disappears within the first year of life. Present data, and also earlier work (Johnson 1973), failed to verify their findings. Feather wear and fading (particularly under tropical sunlight) become subjective criteria after birds have occupied winter ranges for several months.

Based solely on the presence of large bursae (Table 1), most Whimbrels, curlews, tattlers, and some turnstones were about 1 year of age when collected. No bursa was present in curlew 2 and relatively small bursae were found in curlew 4, tattler 2, and turnstones 1–3 (Table 1). Among plovers, bursae were present in 8 of 17 specimens, and ranged in size from 2 to 103 mg (Table 1). The significance of reduced bursae or their absence remains unclear. Possibly such findings reflect birds older than 1 year. Some specimens showed extremely worn juvenal remiges (and often rectrices), and many displayed numerous worn and faded body feathers. Presumably the latter feature represents an incomplete first prealternate molt through which a portion of basic I plumage (and perhaps some juvenal plumage) persists.

It is apparent that research is needed to clarify age evaluation in summering shorebirds. Pending further resolution, the most plausible interpretation of present findings on the bursa and/or plumage is that most specimens were first-year birds. Hence variations in overall feathering (Table 1) probably resulted from individual deviation in the hormonal complex producing alternate I plumage. Certain features pertinent to the plumage and molt of each species studied will be discussed in the remainder of this section.

Golden Plovers.—These birds varied with respect to relative wear of flight feathers (Fig. 1a, 1b). Such variation could result if some first-year birds underwent remige molt during the winter while others did not. This would mean that the moderately worn flight feathers of several plovers (Table 1, Fig. 1b) represented juvenal plumage, but these feathers were not frayed and faded to nearly the extent characteristic of long-distance migrants at approximately 1 year of age (Fig. 2). Definite juvenal primaries in the other species examined were much more abraded, often with little but the rachis remaining distally. Thus it appears that all plovers had molted primaries, secondaries, and some tertials during the fall and winter with variation in primary wear resulting from the interaction of other factors.

Henshaw (1910) stated that the fall migration of Golden Plovers preceded molt, and that the birds began molting heavily after their arrival in the Hawaiian Islands. It is possible that much of the prebasic molt occurs at such major stopping points along the migratory route, with further movement to the south later in the winter. Such movements would result in some birds flying greater distances than others over a vast Pacific range. Johnston and McFarlane (1967) modified Henshaw's findings by noting that some plovers were already undergoing body and wing molt (often one-half or more of the primaries replaced) upon their southbound arrival at Wake Island in August. Johnston and McFarlane's sample probably was made up entirely of adults (no bursae were found, etc.), and thus is not directly comparable to birds lingering on the winter range during the breeding season. Nonetheless such data emphasize individual variability in the timing of prebasic molt. In fact Johnston and McFarlane (1967) found some plovers still molting primaries in December. Little Stints (*Calidris minuta*) and European Oystercatchers (*Haematopus ostralegus*) display similar individual variation in the chronology of primary molt (Middlemiss 1961, Dare and Mercer 1974).

The Golden Plover population at Enewetak in July probably represents a composite insofar as prior behavior on the winter range is concerned. Some birds may have

been resident since fall migration, others likely arrived as a result of winter movements, still others perhaps wintered far to the south and arrested their spring migration at the atoll. Such variables, when combined with individual differences in prebasic molt chronology could readily produce the variation found in primary wear.

Stresemann and Stresemann (1966) studied several specimens of Golden Plovers collected in the tropical Pacific during the boreal summer and concluded that the loss of juvenal wing feathers begins in July and ends around November. As described above, present findings do not support this interpretation. My specimens were molting primaries that showed less than 1 year of use, and thus were referable to a basic feather generation acquired on the winter range.

Relatively unworn barred rectrices (from a molt during the preceding winter) occurred in most specimens, with the middle pair often slightly more worn than the others. Such differential abrasion may well be a result of position—the central feathers being more or less exposed even when the tail is folded. Unbarred (or inconspicuously barred) worn rectrices were found in several birds and presumably represented juvenal plumage (Bent 1929). Whether these feathers can be used as a reliable age criterion should be studied further. There was no obvious correlation between the presence of a bursa and such rectrices. Also Jehl (1973) described a very similar rectrix pattern in Stilt Sandpipers (*Micropalama himantopus*) that had no relationship to either age or sex.

Extensive body molt coincident to the replacement of remiges indicated that many of the plovers were undergoing complete prebasic molt in July. Obviously such a chronology is earlier than the molt schedule of birds on northern breeding grounds. In the case of nonbreeding plumage (basic overall feathering, Table 1) the molt is essentially from one basic plumage into another.

Whimbrels and Bristle-thighed Curlews.—Both species complete a wing molt in the late spring to midsummer period. With the exception of Whimbrel 2 and curlew 7, which were still molting extremely worn juvenal primaries (Table 1), all other specimens had already acquired new primaries, secondaries, and some tertials. I examined a Bristle-thighed Curlew (No. 497562) in the NMNH collection that showed the same molt pattern. The bird was collected at Laysan Island on 15 June 1966, and had molted all primaries through 8 (latter partly sheathed) with 9 and 10 very worn. This individual probably would have finished its primary molt by mid-July (the time when my collections were made). McNeil (1970) described a first-year Whimbrel with newly acquired primaries and secondaries that he collected on 2 July 1965 in Venezuela. These species apparently conform to the Stresemann and Stresemann (1966) concept of first-year birds with a relatively late wing molt (beginning at perhaps 10 months of age), which occurs on the winter range.

In contrast to plovers, the Whimbrels and curlews showed only slight body molt. Hence, these birds were nearing completion of alternate plumage development, and had not yet started prebasic molt. As the latter occurs later than in plovers, prebasic molting may be chronologically similar to that in postnuptial adults. Some curlews had acquired a partial alternate appearance during the preceding winter, others remained in basic plumage. The next molt of the latter birds would be essentially from one basic plumage to another (similar to comparable plovers).

Wandering Tattlers.—These display a wing molt in which the focus appears to be the 6th primary. Prater and Marchant (1975) reported comparable findings in Wandering Tattlers and Polynesian Tattlers (*Heteroscelus brevipes*). Although similar molt patterns occur in other avian groups (Stresemann and Stresemann 1966), these

appear to be the first records of this phenomenon in shorebirds. My small sample of specimens exhibited a sequence of primary molt from 6 through 10, followed in turn by 1, 5, and 4. The primaries being replaced were extremely worn juvenal feathers (Fig. 2).

The question of wing molt pattern in Wandering Tattlers was complicated by skins (all collected on mid-Pacific islands) I examined at the NMNH. Some showed molt commencing at a central focus (as in my specimens), others were molting from primary 1 distally. Perhaps the variation is age-related (Prater and Marchant 1975), with central focus molting restricted to first-year individuals. The matter awaits resolution through further study.

With respect to body plumage, tattlers showed fewer alternate feathers than in any of the other species examined. Virtually all body feathers were of a worn basic generation (with possibly some retained juvenal elements as well). Hence when collected, these birds were molting from one basic plumage to the next with little indication of intervening alternate development.

Ruddy Turnstones.—These varied with respect to the condition of their remiges. Some specimens had renewed these feathers during the preceding winter, others had not (Nos. 1–3; 4–6, respectively, Table 1). Retained remiges were very worn and faded, and referable to the juvenal plumage (Fig. 2).

Max C. Thompson kindly examined the specimens and concluded that Nos. 5 and 6 (Table 1) were definite first-year birds, while the others were probable second-year individuals. Thompson's evaluation was based on his collection of known-age study skins, plus the fact that turnstone breeding coloration tends to intensify with age (pers. comm.). Although specimen 4 seemed more colorful than a typical first-year bird, its remiges and bursa were like those of Nos. 5 and 6 (Table 1). These features suggest that specimens 4–6 represent first-year, and 1–3 second-year birds.

In contrast to the other species examined, turnstones did not demonstrate recent and/or ongoing remige molt. Thus, it appears that young birds retain juvenal wing feathers through their second summer of life. Such a pattern is comparable to short-distance migrants wherein juvenal remiges are replaced during the prebasic II molt (Witherby et al. 1940; Palmer 1967). Ongoing body molt was light (Table 1), and represented the last phases of alternate plumage development. The data suggest that the timing of subsequent prebasic molt in summering turnstones might coincide with that of postnuptial adults.

Acknowledgments

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