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# PLUMAGE-MOLT-AGE RELATIONSHIPS IN "OVER-SUMMERING" AND MIGRATORY LESSER GOLDEN-PLOVERS

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ABSTRACT.—Molts and plumages of Lesser Golden-Plovers (*Pluvialis dominica fulva*) were studied in Hawaii and at Enewetak Atoll, Marshall Islands. Data from collected specimens, color-banded individuals, and field observations have been integrated to trace the prebasic and prealternate body molts, the molt and wear of the primary remiges, and the morphology and molt of the rectrices. Fall juvenal birds have distinctively barred underparts. This juvenal feathering is replaced with adult-like basic I plumage by early winter. The juvenal primaries are not molted in the first winter; the condition of the juvenal rectrices varies individually from no molt to complete replacement during this period. Overall appearance in the first spring ranges from basic to full alternate. The less colorful birds "over-summer" on the wintering range, the others migrate. Migrants retain their juvenal primaries until the prebasic II molt in the next fall and winter, "over-summering" birds begin primary molt during the summer. A few individuals "over-summer" for a second time. These birds generally have well-developed alternate plumages, and again commence primary molt earlier than migrants. The alternative patterns of either migrating or "over-summering" in the first two years, together with the adult molt schedule, produce several age-related combinations of body plumage and primary feather wear. The outermost (sixth pair) rectrices are helpful indicators of age and sex, but exceptions are relatively frequent. Typical juvenal birds have drab, unbarred sixth rectrices; adult feathers are barred and the pattern is sexually dimorphic.

Although the insular Pacific constitutes a major wintering range for shorebirds, there have been relatively few studies of them in this geographic region and long-term research is notably lacking. In August 1979, we began ecological and behavioral investigations of the Lesser Golden-Plover (*Pluvialis dominica fulva*) in Hawaii, emphasizing the monitoring of marked individuals through consecutive winters (Johnson et al. 1981). Molt cycles in the plover are complicated by "over-summering" behavior (McNeil 1970, Johnson 1973) in which some young birds remain on the wintering grounds for one or two boreal summers before their first northward migration. This produces several age-related patterns of plumage development and primary feather wear. We intend here to present plumage and molt data obtained in Hawaii through the spring of 1982, and to integrate this information with earlier findings from Enewetak Atoll (Johnson 1977, 1979). This treatment should prove useful to workers concerned with age and sex determination in plovers and other shorebirds. We hope it will also have significance in broader contexts such as the taxonomic status of this subspecies and the behavioral adaptations associated with long-distance migration in shorebirds.

## STUDY AREAS AND METHODS

Most of the findings reported here are from two study sites located on the northeast coast of Oahu, Hawaii (approximately 21°N, 158°W). Additional data were obtained at Enewetak Atoll, Marshall Islands (approximately 11°N, 162°E). Work began in Hawaii in August 1979 and is ongoing; observations and collections at Enewetak were made from 9 June–6 July 1970, 4–17 July 1973, and 16–28 November 1978.

The primary study site in Hawaii was Bellows Air Force Station (BAFS) located near the town of Waimanalo. Bellows is an inactive military reservation of about 600 ha with an abundance of ideal plover habitats such as lawns, pastures, and unused runways. The secondary site was on the nearby Kaneohe Marine Corps Air Station (KMCAS), an active base covering about 1,100 ha. Approximately 300 plovers winter at BAFS, and at least 600 at KMCAS.

During the period from 29 September 1979 through 12 April 1982, we captured 70 plovers

in mist-nets at BAFS and banded each bird with a U.S. Fish and Wildlife Service aluminum band plus a unique combination of from one to three plastic color-bands that allowed individual field recognition. (The plastic bands were sealed by placing a small drop of acetone under the overlapping portion of the band with a fine-gauge hypodermic syringe. To date, we have no evidence of band loss.) At the time of banding, descriptive notes were made as to the individual's overall plumage (Table 1), and the molt of the primary remiges and rectrices.

Plovers have 11 pairs of primary remiges and 6 pairs of rectrices. The vestigial 11th primary (Witherby et al. 1940) was ignored and only features pertaining to the 10 large primaries are described. The flight feathers were numbered conventionally, the #1 primary being the innermost in the series, and the #1 rectrices being the central pair. Primary molt was scored on the right wing using Ashmole's (1962) system wherein: 0 = an 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 the sheath. Thus, a total score of 0 indicates worn primaries with no molt underway; from 1 to 49 represents progressive degrees of molt and feather growth; and 50 indicates 10 new, fully developed primaries.

Of the total banded, 61 birds were located in the same season subsequent to release and each was seen repeatedly (generally, at least once per week) until spring migration. In the falls of 1980 and 1981, most of the marked plovers returned (one-year return rates based upon the total banded in each previous winter were 83.3 and 90.0%, respectively) to BAFS from the arctic nesting grounds. These birds were seen during subsequent winters and their plumage changes recorded using the categories shown in Table 1. Thus, we obtained a chronicle of the molting cycles in known individuals over long periods of time which for some individuals included three consecutive wintering seasons.

To supplement data obtained from marked birds, we monitored the cycles of prebasic and prealternate molting in about 400 plovers along two automobile census routes (4.3 km at BAFS and 7.1 km at KMCAS). The routes were run weekly from 17 August 1979 through 21 April 1980 (just before migration), and each plover encountered was assigned to one of the plumage stages shown in Table 1. Our studies of marked plovers have demonstrated that territorial individuals occupy the same territories daily for the entire wintering season (Johnson et al. 1981). Since at least one-half of the plovers along the census routes were territorial, we were in effect monitoring many of the same birds throughout the period of observation.

TABLE 1. Lesser Golden-Plover body plumage development.

| Stage[a] | General features[b] |
|---|---|
| Basic | Buffy/brown coloration overall; throat, cheeks, underparts without black feathering; superciliary and neck stripes faint to absent. |
| Flecked alternate | Buffy/brown overall, but a few black feathers present on the breast and belly; superciliary and neck stripes faint. |
| 1/4 alternate | Black feathers scattered on the underparts, throat and cheeks; superciliary and neck stripes faint to moderately bright; scattered bright gold/yellow feathers on crown and back. |
| 1/2 alternate | Proportionate increase in black feathering and gold/yellow coloration; superciliary and neck stripes moderately bright to bright. |
| 3/4 alternate | Proportionate increase in black feathering and gold/yellow coloration; superciliary and neck stripes sharply delimited and bright; obvious buffy feathering on otherwise black cheeks. |
| 3/4+ alternate | Intense coloration overall (as in full, below), but a few scattered buffy feathers remaining on cheeks. |
| Full alternate | Intensely colored with crisp delimitation of white/black/gold patterning, no buffy feathers on cheeks. |

[a] In the order listed, the stages reflect the prealternate molt; the reverse order represents the prebasic molt.

[b] Females have a less colorful alternate plumage than males (see section on prealternate molt), but this dimorphism is evident only among adult birds in the late spring. During most of the wintering cycle we know of no reliable field criteria for distinguishing the sexes. With certain exceptions (collected specimens and some of the color-banded individuals), our data represent birds of unknown sex. Therefore, we have used a common system (table above) for both sexes with the final stages (3/4+ and full alternate) representing the intensely colorful alternate plumage of males. Males and females share the plumage stages through 3/4 alternate, and our descriptions of female plumages must be interpreted in that context. For example, when we describe a female in 1/2 alternate we mean that *she has the same appearance as a male at the 1/2 alternate stage*. We do not mean that she has acquired 1/2 of the feathering characteristic of the female alternate plumage. In fact, since females do not become as colorful as males, a female in our 1/2 alternate stage would be nearing her complete alternate development.

Eighty-three plovers were collected from BAFS at intervals during the winter of 1979–1980. These furnished information on age and sex relative to body plumage development, and on condition and/or molt of the primaries and rectrices. An intact wing and the rectrices were retained from each specimen for further study. The remainder of the carcass was used for work presently underway on levels of body fat relative to the energetics of long-distance migration.

As used here, we define our terms expressing *age* as follows: (1) *Juvenal*—Refers to approx-

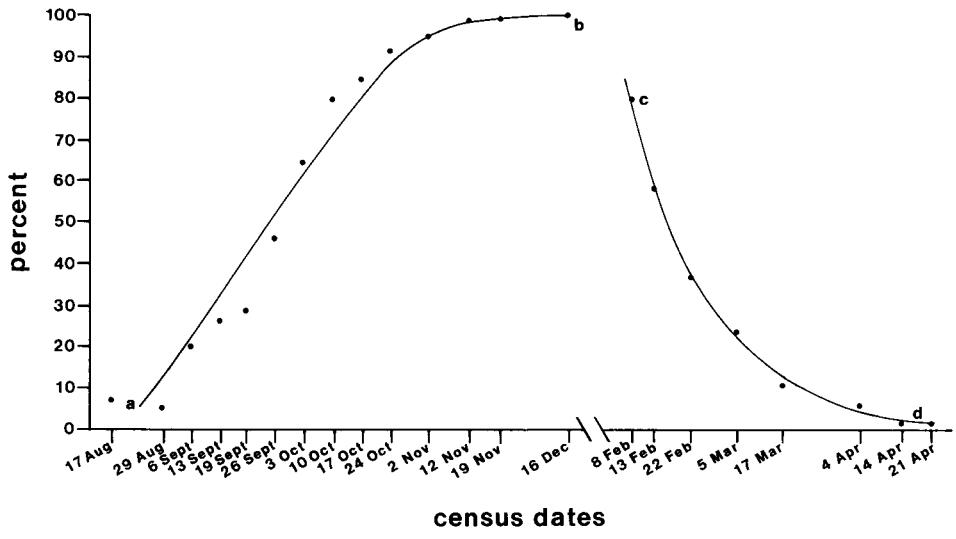


FIGURE 1. Percent of basic plumage birds among wintering Lesser Golden-Plovers at Bellows Air Force Station and Kaneohe Marine Corps Air Station. [a] Most of the birds returned to the study sites in August. Returning birds were in prebasic molt and had varying amounts of alternate plumage remaining. August census counts indicated flock composition to be approximately: 60% ¼ alternate plumage, 25% flecked alternate plumage, 10% ½–¾ alternate plumage, and 5% basic plumage. Most of the basic plumage birds were not migrants but rather "over-summering" birds (see text). [b] Past this date, only basic plumage was found until late January. By that time, subtle indications of the prealternate molt were noted with slightly brighter gold/yellow tones dorsally and slightly greater patterning on the head and neck. [c] Field census conditions made it impracticable to remove a bird from the basic plumage category until obvious flecks of dark coloration appeared ventrally. This occurred in early February when approximately 20% of the plovers showed the first flecking. [d] The line does not go to zero because some first-year birds remain in basic plumage. The curves were fitted by eye.

imately the first 10 months of the bird's life; it is applied to these birds during the period from their arrival on the wintering grounds in one calendar year until their departure on spring migration in the following calendar year. (2) *First-year bird*—Time of spring migration was used as a landmark after which a "juvenal" was renamed a "first-year bird" (i.e., denoting the first migratory cycle after hatching). At this juncture, such a bird either migrates or remains on the wintering grounds and "over-summers." First-year status was considered to end with the replacement of juvenal primaries in the fall and early winter of the second wintering season at about 16–17 months of age. (3) *Adult*—After replacement of the juvenal primaries, the individual was termed an "adult." Subdividing adults into age groups was impracticable except that a few individuals could be recognized as "over-summering." Presumably, these were *21-month old adults* (this is consistent with patterns of primary molt and wear described later) most likely representing some fraction of those first-year birds that had "over-summered" in the previous season (i.e., some birds "over-summer" for two consecutive summers). Only a relatively small proportion of the 21-month old adults over-summer, and probably this behavior occurs rarely, if at all, past this age. (4) *Postjuvenals*—A group comprised of first-year birds and adults, as would occur on the wintering grounds before first-year birds complete primary molt. These terms are discussed further in footnote a, Figure 4.

## RESULTS AND DISCUSSION

### PLUMAGE AT FALL ARRIVAL AND THE PREBASIC BODY MOLT

Fall sightings of banded birds plus field observations of unmarked migrants showed that postjuvenal plovers returned to the Hawaii study sites from early August until mid-September. Twenty-three of 35 marked birds sighted in fall 1980 and 27 of 39 sighted in fall 1981 were first seen in August, with most arriving between 8–26 August. Returning birds retained differing amounts of alternate plumage. Relative to the stages in Table 1, almost all birds (approximately 85%) ranged from flecks of alternate to ¼ alternate; the remaining individuals were mostly ½ alternate with an occasional bird approaching ¾ alternate. As the prebasic molt progressed, about 50% of the birds attained basic plumage by the end of September, about 95% by the end of October, and essentially all birds by mid-November (Fig. 1).

The plumages of August migrants clearly indicated that prebasic molting had begun on the

nesting grounds. Marked birds that were last seen in well-developed alternate plumages at the time of spring migration returned to Hawaii in plumages ranging from flecked alternate to ½ alternate. This confirms Sauer's (1962) and Johnston and McFarlane's (1967) observations at St. Lawrence Island and Wake Island, respectively, and contradicts Henshaw's (1910) claim that fall migration precedes molt. Sauer (1962) found that male plovers began body molt during incubation and that much of their breeding coloration was lost by the time of hatching. His photographs of representative males, taken on 18 and 29 July, depict birds equivalent to our ¼ alternate stage (Table 1). Sauer termed this molt in males an "eclipse molt," but more properly it should be regarded as the beginning of the prebasic molt. Since alternate plumage is less colorful in females than in males (see section on prealternate molt) and changes accompanying molt are less distinct, Sauer was unable to determine whether comparable molting was underway in females. That such molting does occur was evident from our observations of marked females during fall arrival in Hawaii.

Based upon the chronology of the breeding cycle (Dementev and Gladkov 1951, Sauer 1962, Portenko 1972) we assumed that prebasic molting began about 1 July. Most of the marked birds, and also the majority of unmarked birds on our census routes, completed the prebasic molt from mid-September to mid-October (Fig. 1); thus, its duration was about 2.5 to 3.5 months. A few birds in basic plumage were present during August counts (Fig. 1). Some of these were "over-summering" birds (it was impossible to exclude these from our censuses since they intermingled with migrants and could not be distinguished from them), others were possibly first-year migrants. "Over-summering" plovers often developed little or no alternate plumage, thus its presence might be of short duration during the prebasic molt. First-year migrants developed varying amounts of alternate feathering in the spring (see section on prealternate molt), but subsequent events on the nesting grounds were unclear. Observations are needed in the arctic to determine whether first-year birds are non-breeders or less successful breeders, and if so, whether their prebasic molting prior to southward migration might be more extensive than that of adults.

Adult plovers preceded juvenals in fall migration by about six weeks in Hawaii (Johnson et al. 1981); comparative data from Enewetak are lacking. In 1979 (data are unavailable for 1980 and 1981), we encountered no juvenal birds until 26 September on which date they appeared at both BAFS and KMCAS. The juvenal body plumage is characterized by a distinctive pattern of ventral barring (Prater et al. 1977). Additional criteria helpful in identifying juvenals were: a relatively plain and unpatterned head and neck lacking remnants of the superciliary line and neck stripe prominent in the alternate plumage; and fresh, dark gray primary remiges, which were uninterrupted by gaps caused by missing feathers (i.e., postjuvenals molt their primaries in fall and winter, juvenals do not; gaps, or lack thereof, could often be seen when a bird was flushed at close range). Juvenals began their first prebasic body molt on the wintering grounds, and acquired the first basic plumage by early December.

As the prebasic molt of adults neared completion, the feathering of the head and neck provided the last evidence of earlier breeding coloration. Although the white feathers of the superciliary line and neck stripe were replaced by buffy feathers, the latter continued to produce a pattern that was discernible for several weeks. With time, this pattern faded and by early December relatively little of it remained. At this point, the basic body plumages of adults and juvenals were essentially identical and the two groups could not be distinguished unless the birds were in hand.

### PRIMARY MOLT

We found that juvenal plovers did not molt their primaries in the first winter, and that many older birds deferred primary molt until reaching the wintering grounds in the fall. Similar observations were reported by Henshaw (1910), Dementev and Gladkov (1951), Stresemann and Stresemann (1966), and Kinsky and Yaldwyn (1981). Molting of inner primaries before migration evidently occurs in some individuals (Stresemann and Stresemann 1966, Johnston and McFarlane 1967, Prater et al. 1977), but descriptions are fragmentary and it is unknown whether such birds might represent a particular age class. Kinsky and Yaldwyn (1981) speculated that these are "immature non-breeders"; more specifically, we feel that they are likely to be first-year migrants. Present data are insufficient to resolve the matter; as mentioned earlier, work is needed to clarify the summer cycle of this generation. August specimens showed clearly that primary molt frequently begins on the wintering grounds. Among 17 birds collected through 1 September, 6 were not yet molting primaries and the others were in early stages of molt (Fig. 2).

The chronology of primary molt can be approximated from Figure 2. Plovers varied as to when they began losing primaries, ranging from early August to early September. Assuming that individuals who started earliest would

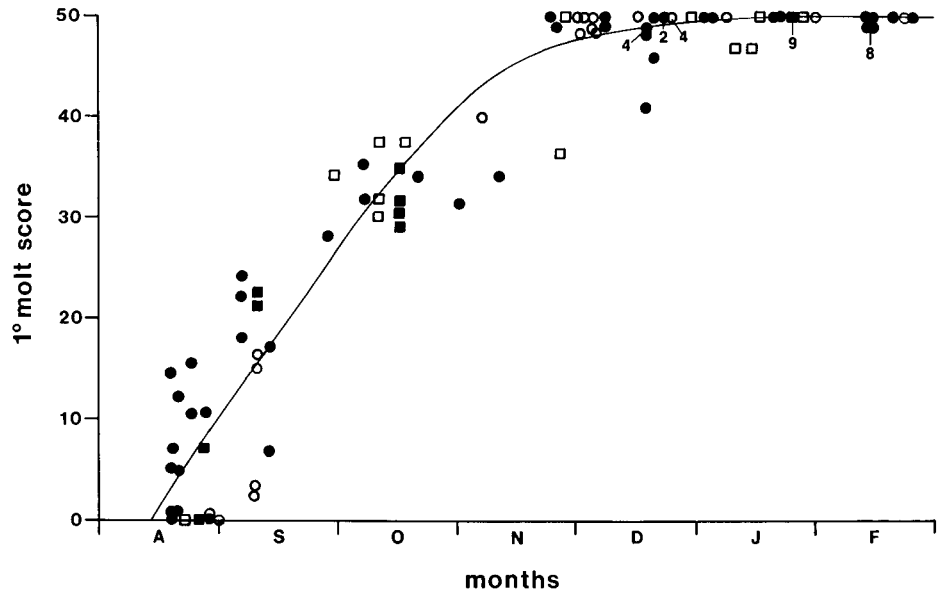


FIGURE 2. Primary molt scores of Lesser Golden-Plovers wintering in Hawaii. Closed circles represent birds either banded or collected by us at BAFS. Closed squares are specimens from the collection of the Hawaii Division of Forestry and Wildlife, Honolulu; most of these were collected at BAFS in 1969–1970. Open circles show specimens from the B. P. Bishop Museum, Honolulu, which were collected at various sites in the Hawaiian Islands. Open squares are specimens from the Brigham Young University-Hawaii Campus Museum of Natural History; these were collected near Laie and Kahuku on the northeast coast of Oahu. Data are shown through February only because after 11 February all adult plovers observed had scores of 50. The sample from 1 March through migration at the end of April consisted of 61 collected or netted by us, 10 Hawaii Forestry and Wildlife collection, 6 BYU-HC Museum of Natural History collection, 4 B. P. Bishop Museum collection. Where scores overlap and individuals cannot be clearly shown, the number next to the data symbol or cluster of symbols indicates how many birds are represented. The curve was fitted by eye.

also finish earliest and vice versa, primary molt durations ranged from about four to five months (i.e., early August to late November; early September to early February). In all of the specimens we examined, prebasic body molt was completed before primary molt was completed (often by several weeks).

In juvenal birds, we found fresh, unworn primaries in the fall. Since these were not molted during the winter they became very worn by spring (Fig. 3a, b). Among postjuvenals collected in the early fall (17 birds from 17 August through 13 September 1979) and adults collected in the spring (30 birds from 19 March through 27 April 1980), primary wear varied individually. This was particularly evident in the fall when the samples defined three categories: primaries slightly worn, moderately worn, very worn (Fig. 3c, d, e). In the spring, primaries varied from slightly worn to unworn. These variations appeared to be age-related and to reflect different patterns of migratory and "over-summering" behavior. Before considering the nature of these patterns, two additional observations must be mentioned briefly. Relatively few plovers "oversummered" on our study sites in Hawaii; most of the first-year birds acquired alternate plumage (see section on prealternate molt) and migrated. "Over-summering" birds (whether first-year or older) began primary molt in June or July.

This leads us to propose the relationships shown in Figure 4. Major points are: (1) First-year birds that migrate molt all or most of their juvenal primaries on the wintering grounds during their second prebasic molt (Fig. 4, pattern 2). Our data were inconclusive for testing the possibility that these birds are nonbreeders and replace some primaries before southward migration. Hence, fall migrants with very worn primaries (Fig. 3e) are returning first-year birds and their primaries are elements of the juvenal plumage (Fig. 4, pattern 2). (2) Since "over-summering" birds start primary molt in mid-summer, they finish this molt earlier than migrants (Stresemann and Stresemann 1966, Johnson 1977, Kinsky and Yaldwyn 1981). There appeared to be a one- to two-month differential between the two groups. Therefore, a first-year "over-summering" individual who migrates in the next breeding cycle as a 21-month old adult (Fig. 4, pattern 3) will be using older primaries than a 21-month old adult that

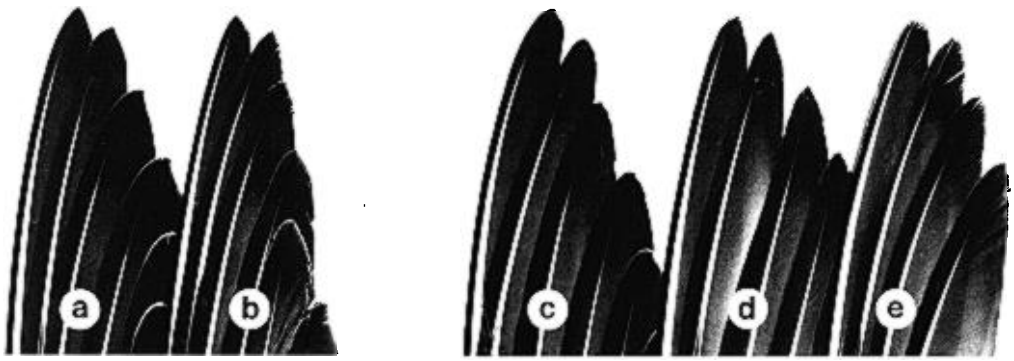


FIGURE 3. The outer primaries of Lesser Golden-Plovers showing various degrees of wear. Juvenal primaries are unworn in the fall (a), very worn by spring (b). Fall adults show either slight wear (c) or moderate wear (d). The former indicates the bird did not "over-summer" in the previous calendar year, the latter indicates that it did. First-year migrants return to the wintering grounds with very worn juvenal primaries (e). In spring adults (not shown here), those that did not "over-summer" in the previous calendar year have unworn primaries like (a), while those that did "over-summer" have slightly worn primaries like (c). See text for additional details.

previously had been a first-year migrant (Fig. 4, pattern 2). In either spring or fall, this would cause more wear of the primaries in the former as compared to the latter. A similar pattern also leading to greater primary wear would occur in those 21-month old adults who "over-summer" for a second time (Fig. 4, pattern 4). Hence, moderate primary wear in fall migrants (Fig. 3d; Fig. 4, some of the birds in pattern 5) should be referable to "over-summering" in the previous calendar year. A one- to two-month difference in wing molt seemed inadequate to produce a differential in primary wear. However, limited experiments with exposure to sunlight (conducted in Hawaii using remiges from collected plovers, unpubl. data) showed significant destructive effects over relatively short periods; hence, sunlight may account for the variation described. (3) It follows that any spring pre-migratory bird with unworn primaries (Fig. 4, patterns 2 and 5) or any fall migrant with slightly worn primaries (Fig. 3c; Fig. 4, some of the birds in pattern 5) must be an adult who had not "over-summered" in the previous calendar year.

The idea that first-year birds fly round-trip to the nesting grounds on worn juvenal primaries initially seemed questionable. However, flying per se may cause less feather wear than long exposure to intense tropical sunlight. Our sunlight exposure data support this interpretation as does the observation that juvenal birds arriving in the fall after one southward flight of at least 4,000 km have fresh, darkly colored primaries without discernible wear. Furthermore, adults returning in the fall often show only slight primary wear despite the round-trip just completed (Fig. 3a, c).

Greater primary wear as an indicator of "over-summering" behavior in the previous calendar year, together with the fact that relatively few plovers "over-summer" on the study sites should produce the following relationships: (1) most adults returning in the fall would have slight primary wear and only a few would show moderate wear, (2) most spring adults would have unworn primaries and only a few would show slightly worn primaries. Our data were insufficient to evaluate the first relationship. We had only one sample (14 collected specimens) from the fall arrival period, and this group was divided evenly between slight and moderate primary wear. These negative findings probably reflect the presence of transient birds in the fall populations on our study sites. Some of the birds we collected may have been en route to other wintering areas farther south in the Pacific where "over-summering" behavior may be more common (see additional comments in the last section of this paper). The second relationship was confirmed over three consecutive springs. From March through mid-April 1980–1982 (before spring migrations, no transients were present), we examined a total of 60 birds (both collected and netted specimens), and the ratio was 56 with unworn to 4 with slightly worn primaries.

### PREALTERNATE MOLT

As briefly mentioned in Figure 1, the first indications of prealternate molting were seen in late January. They consisted of slightly brighter coloration on the back and crown combined with faint suggestions of the incoming superciliary and neck stripes. These initial changes were subtle, but molting soon became obvious

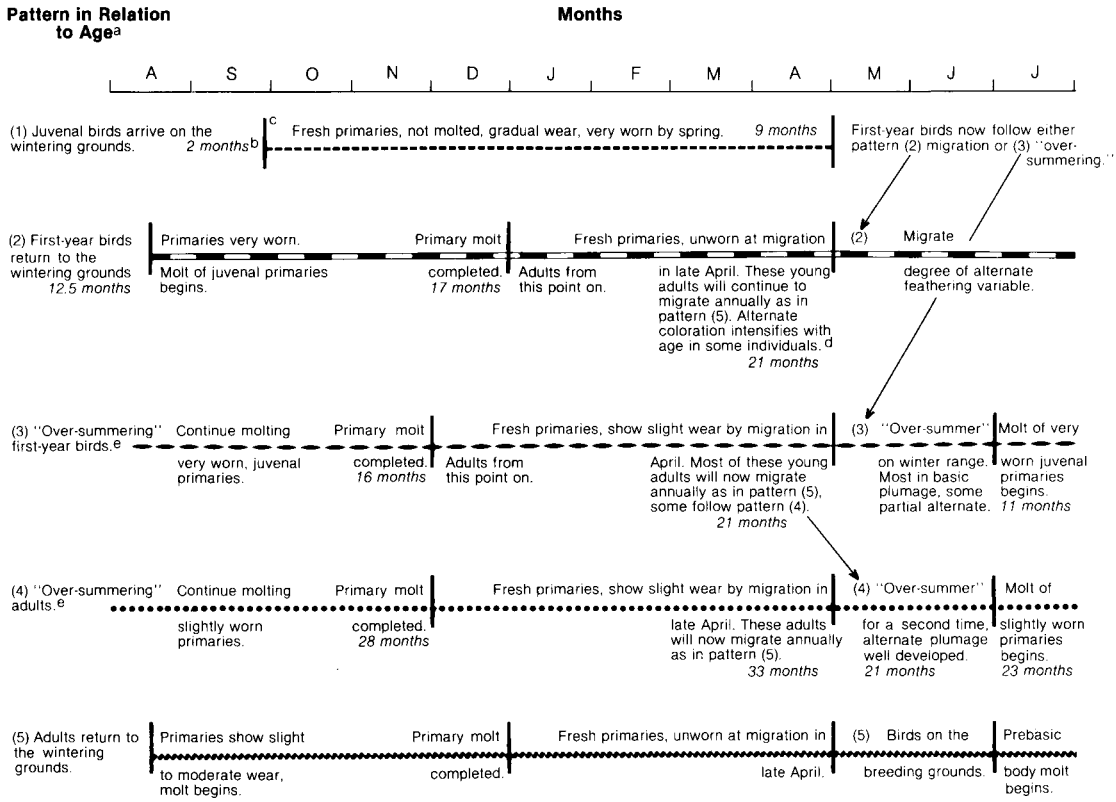


FIGURE 4. Patterns of primary molt in Lesser Golden-Plovers wintering on Oahu and Enewetak. [a] Early fall arrivals of first-year (2) and adult birds (5) followed by the later arrival of juvenal birds (1) combine with "over-summering" birds (3) and (4) to make up a rather complex wintering assemblage. The various groups can be recognized, but only over certain periods of time. The juvenal body plumage (see text) combined with fresh primaries clearly indicate age through the fall months. In winter (as juvenals acquire their first basic body plumage and older birds complete their primary molt) identification of juvenal plovers often becomes subjective. By spring, juvenals are again distinctive because their worn juvenal primaries obviously contrast with the fresh primaries of adults. With spring migration, juvenal birds become first-year birds in our system of terminology. All first-year birds (whether migratory or "over-summering") can be identified until their juvenal primaries have been replaced in November or December, thereafter specific age becomes unclear and birds must be termed adults. Only one subgroup of adults can be recognized and only for a relatively brief period of time. The "over-summering" 21-month old adults (pattern 4) can be identified during the summer from their slightly worn primaries. This distinction is lost in the fall with the influx of other adults returning from the breeding grounds. Primary wear varies among returning adults (pattern 5). Slight wear indicates that the bird did not "over-summer" in the previous calendar year, while moderate wear shows that it did (see text). [b] Approximate ages of birds in months at representative points in the cycle. [c] Vertical lines show the approximate times when particular events occur. [d] Comments pertaining to other plumage features are given where pertinent. [e] No "over-summering" birds were collected on Oahu; hence, these portions of the diagram are based on data obtained at Enewetak. This seems reasonable because the resultant overall patterns fit the Oahu findings, and the plumages of "over-summering" birds on Oahu (as viewed in the field) correspond with those at Enewetak.

as the first black feathers appeared on the underparts (flecked status, Table 1). The gradual replacement of basic plumage by alternate plumage is represented by the descending curve on the right hand portion of Figure 1. The latter shows that prealternate molt occurred within the wintering flock over three months from late January through departure in late April. Individually, however, molts were briefer and many birds along the census routes acquired full alternate plumage by early April (i.e., after about two months of molting).

In an effort to further detail the prealternate molting patterns of individuals, we monitored 25 marked birds in the spring of 1980, recording each bird's molt status from the point when the first ventral black flecking appeared until migratory departure. Many of these same birds, plus others banded subsequently, were similarly monitored in the springs of 1981 and 1982. Interpretations of the resultant data have been complicated by inherent difficulties of age and sex determination. Although juvenal birds can be identified in the fall and early winter from their fresh primaries and barred underparts, and again in the spring when their primaries show much greater wear than those of adults, age determination in birds banded dur-

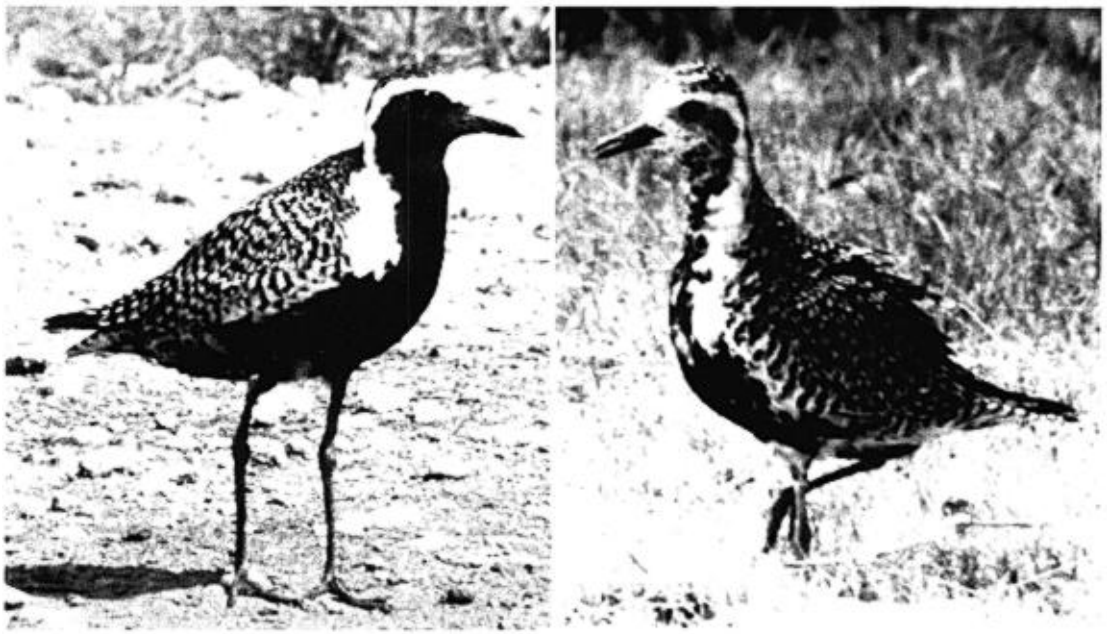

FIGURE 5. Sexual dimorphism is marked at the time of spring migration from Hawaii. A typical male (left) shows ¾+ to full alternate plumage; a typical female (right) shows ½ alternate plumage. The same dimorphic features have been reported from the breeding grounds in *P. d. fulva* (Sauer 1962), and also in *P. d. dominica* (Van Tyne and Drury 1959). Both photographs were taken in late April at BAFS.

ing mid-winter is often subjective. The most accurate external sex criterion is the alternate plumage of late spring when adult males (and some juvenal males) are more intensely colored than females. Observations of this dimorphism over consecutive spring periods clearly revealed the sex of many of our color-banded birds. The only other known indicator of sex is the appearance of the sixth rectrix, but this is often misleading (see section on rectrices). As a further variable, we found that the first two or three prealternate molts in a plover's life may be progressively more extensive, with the result that a bird thought to be a female may later prove to be a male.

We expect these complications to be clarified as we continue to monitor the marked population, which will permit a more detailed treatment later. For the present, the following general features of prealternate molting can be described: (1) The degree to which alternate feathering developed during the first prealternate molt in juvenals was highly variable, and this variability may also extend to the second and third prealternate molts. For example, a marked female showed progressively longer molting periods and increased development of alternate plumage in each of three springs—1980, molting for only five days before migration, flecked appearance at departure; 1981, 12 days, ¼ alternate; 1982, 26 days, ½ alternate. Similar patterns were recorded for other individuals of both sexes. By contrast, in some juvenal birds the first prealternate molt produced plumage indistinguishable from that of adults. From 16 through 27 April 1980, we collected seven juvenals (two females and five males, all with worn primaries and cloacal bursae) that were adult-like in appearance and could not have been identified as juvenals in the field. Plumage development in the females was at the ½ alternate stage, while in males it ranged from ¾ to full alternate (Table 1). Still other juvenals underwent much less prealternate molting (or none at all) and remained in basic or flecked plumages. These birds generally "over-summered" on the wintering grounds, while those juvenals that achieved greater degrees of alternate feathering generally migrated. Small numbers of drably colored juvenals (around 15 birds) remained at BAFS during the summers of 1980–1982. (2) Adult males typically achieved at least ¾+ alternate feathering (most were in full alternate) before spring departure (Fig. 5). Collected specimens clearly indicated that males were the first birds to show evidence of prealternate molting (ventral flecking) in the spring with the first few flecks usually visible by mid-February. Five marked males monitored in 1980 progressed from the first flecks to full alternate plumage in from 66 to 68 days. (3) Adult females typically were in the ½ alternate plumage stage (some approached the ¾ alternate stage) at the

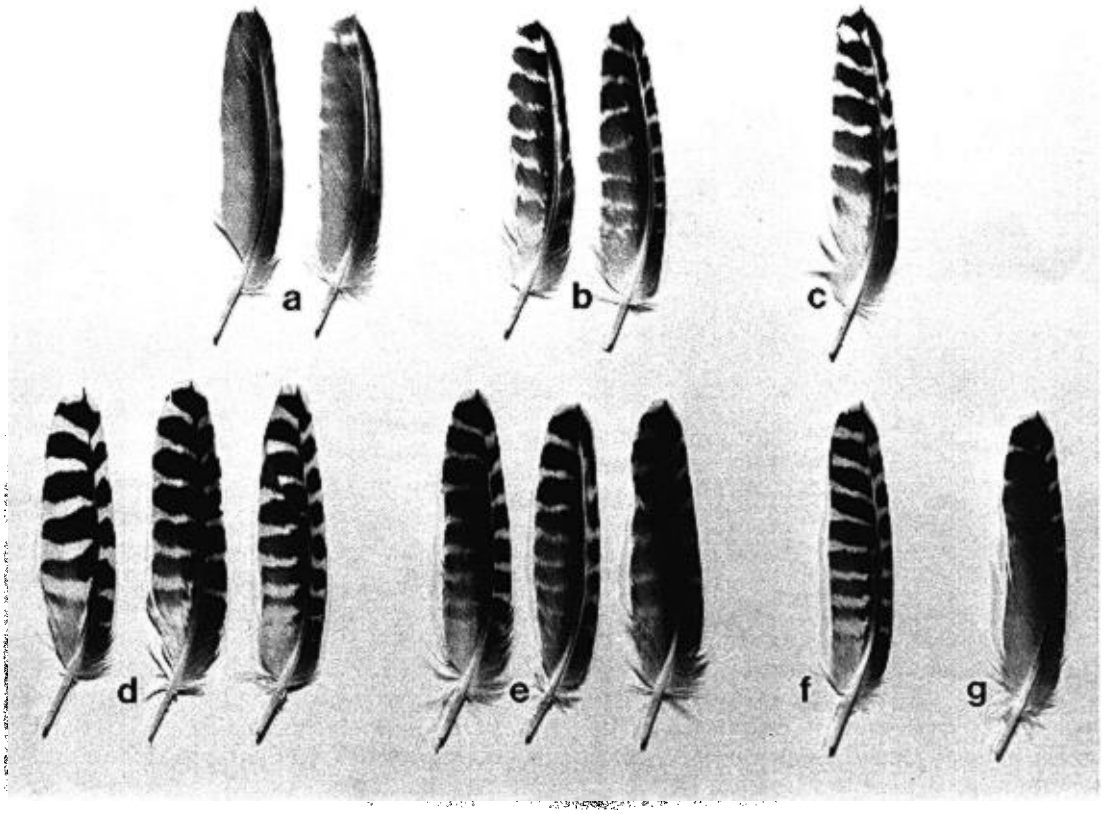


FIGURE 6. Representative sixth rectrices from Lesser Golden-Plovers. The typical juvenal feather is drab and unpatterned (a) while the adult feather is barred and colorful (d–g). Some juvenal birds have barred feathers which approach (b) or equal (c) adult characteristics. Typical adult males (d) have strongly barred feathers, in typical adult females (e) the barring is less distinct. Atypical females (f) and males (g) are relatively frequent. See text for additional details.

time of spring departure (Fig. 5). Most females began to show flecking about one month later (mid-March) than males, and thus were molting for a shorter period (altogether about five to six weeks) before migration. (4) Instances of lengthy, slow molt were noted. Two marked individuals monitored in 1980 required 44 and 57 days, respectively, to progress from the first flecking to only a ¼ alternate plumage at migration. In both cases, these patterns were probably first prealternate molts. Further data are unavailable for the first bird, but the second was seen on 8 April 1982 in ¾+ alternate plumage. The latter would be consistent with an adult male and would imply that in 1980 the bird was a juvenal.

RECTRICES

Johnston and McFarlane (1967) first called attention to the sixth rectrices (outermost pair) as a sexually dimorphic feature in *P. d. fulva,* but did not recognize that these feathers also were a useful indicator of age. Kinsky and Yaldwyn (1981) correctly described the juvenal sixth rectrix as typically drab and unpatterned whereas the adult feather tends to be conspicuously barred. They went on to conclude that the sixth juvenal rectrix is a definitive criterion of age through the first year of life since it is readily identifiable and not lost until a full molt in the bird's second summer and fall (i.e., from about 11 to 16 months of age). We agree that juvenal plovers tend to have drab sixth rectrices, but we also found considerable individual variation such that in some birds these feathers were adult-like. Also, the timing of rectrix molt varied, with some birds replacing their rectrices during their first winter. Thus, our data do not substantiate Kinsky and Yaldwyn's uncomplicated interpretations of the sixth juvenal rectrix.

From 11 through 26 November 1978, O. W. Johnson and M. L. Morton collected 23 juvenals (all with fresh juvenal primaries, and cloacal bursae ranging in weight from 46 to 376 mg) at Enewetak Atoll. Of these, 15 had typical drab juvenal sixth rectrices, 6 had barred rectrices approaching adult patterns, 1 had a

TABLE 2. Rectrix molt and other features in juvenal Lesser Golden-Plovers collected at BAFS, spring 1980.

| Specimen no., sex, bursa wt. (mg) | Date collected | Rectrix molt[a] | Appearance 6th rectrix[b] | Appearance overall plumage[c] |
|---|---|---|---|---|
| 1, male, 156 | 19 March | 1–3 | juvenal | flecked |
| 2, male, 94 | 19 March | 1–6 | adult | flecked |
| 3, male, 130 | 9 April | 1–2 | juvenal | flecked |
| 4, male, 117 | 9 April | 1–4 | juvenal | 1/4 |
| 5, female, 42 | 16 April | 1–3 | juvenal | 1/2 |
| 6, female, 42 | 16 April | 1–6 | adult | 1/4 |
| 7, male, 45 | 23 April | 1–2 | juvenal | 3/4+ |
| 8, male, 90 | 23 April | 1–4 | juvenal | 3/4 |
| 9, female, 49 | 23 April | 1–5 | juvenal | 1/2 |
| 10, male, absent | 23 April | 1–6 | adult | 3/4+ |
| 11, male, 23 | 27 April | 1 only | juvenal | 3/4 |
| 12, male, 11 | 27 April | 1–2 | juvenal | flecked |
| 13, male, 42 | 27 April | 1–6 | adult | full |

[a] Numbers show which of the six pairs had been molted or were in molt; numbers not shown are juvenal feathers still in place. No particular order of feather loss is implied. Molt begins centrally and progresses laterally with irregularity in the sequence of loss. The members of a given pair often develop asymmetrically.
[b] In accordance with the photographs shown in Figure 6.
[c] In accordance with the terms in Table 1.

drab sixth rectrix on one side with the contralateral feather barred, and 1 (otherwise juvenal in appearance, and with a bursa weighing 216 mg) had adult-like rectrices (Fig. 6a–c). At BAFS, we collected four juvenals (bursae ranging from 24 to 127 mg) in the fall from 3 through 28 October 1979. Of these, three had typical juvenal rectrices and one had barred rectrices. Thus, two-thirds (18 of 27) of the birds in our combined sample from Hawaii and Enewetak had typical juvenal sixth rectrices; the others had outer rectrices that could have been mistaken for adult feathers. According to Kinsky and Yaldwyn (1981) the latter mistake is unlikely since any barring that does occur in the juvenal sixth rectrix is restricted to the inner (wider) vane, the outer vane remaining uniformly colored. In this we disagree, having often found the barring to extend across both vanes (Fig. 6b, c).

Our data from juvenals in the mid-winter are limited to four specimens (bursae ranging from 73 to 262 mg) collected at BAFS (2 on 18 December 1979 and 2 on 11 February 1980); three had typical and one had barred sixth juvenal rectrices. Although the sample was small, it was significant in that it revealed the onset of molt of the juvenal rectrices. One of the December birds had the central pair of rectrices in pin stage, the other bird was not molting; both February birds were molting rectrices, one the central two pairs, the other the central four pairs. In some birds (see below) this first winter molt of rectrices will progress to include the fifth and sixth pairs.

We collected 13 juvenals at BAFS in the spring from 19 March through 27 April 1980 (all with very worn primaries, and all but one with cloacal bursae ranging from 11 to 156 mg). Some of the birds still had their juvenal sixth rectrices, in others rectrix molt was complete and the sixth rectrices were fresh and adult-like in appearance. The status of rectrix molt and other plumage variations among juvenals in their first spring (when they will either migrate or "over-summer"), is evident in a summary of the 13 birds (Table 2). Development of the alternate plumage is not correlated with the appearance of the sixth rectrix. Birds with well developed breeding coloration may still retain a juvenal sixth rectrix (as nos. 7 and 8) and vice versa (as nos. 2 and 6). Based on alternate plumage development, we predict that specimens 5, 7–11, and 13 would have migrated, specimens 4 and 6 may have migrated, and specimens 1–3 and 12 would have "oversummered." "Over-summering" birds continued rectrix molt during the summer (see below), but rectrix molt in the migrants remains to be clarified. One of three first-year migrants collected in early fall at BAFS still retained faded and worn juvenal fifth and sixth rectrices, while the other four pairs were fresh and had obviously been molted; the other two birds had molted all their rectrices earlier.

No "over-summering" first-year plovers were collected at BAFS or KMCAS; however, 14 specimens were taken at Enewetak from 6 to 12 July 1973 (all but 2 had started molt of the worn juvenal primaries, and 8 still had cloacal bursae ranging from 2 to 103 mg). Four of the birds had completed rectrix molt, nine were in various stages of rectrix molt, and one had not yet started. Overall, the Hawaii-Enewetak collections show considerable individual variability with most birds starting to molt their juvenal rectrices (in some cases all of the rectrices) before spring migration; and a few birds deferring this molt until summer (i.e., at approximately one year of age).

Three specimens of "over-summering" 21-month old adults (all with primaries slightly worn, two in primary molt and one not yet started, no cloacal bursae) were collected at Enewetak from 6 to 12 July 1973. Unfortunately, only the outer two or three (pairs 4–6) rectrices from one side of each bird's tail were saved. Each bird had a barred adult-like sixth rectrix which was faded and presumably referable to the rectrix molt about one year earlier. With these limited materials we could not determine the overall status of rectrix molt when the birds were collected.

Rectrix molt in 57 adults collected at BAFS showed so much individual variation that we were unable to detect patterns or chronologies, and only some general comments can be made. Like Johnston and McFarlane (1967), we found rectrix molt to be centrifugal from pair #1 and disorderly as to the sequence of rectrix loss. Various degrees of asymmetry were relatively common: for example, one feather of a pair might be in pin stage, the other one-half or more grown, or the pair might consist of one fresh and one old feather. The array of variations produced tails wherein at least two, and in some birds possibly three, generations of rectrices (as judged from relative degrees of fading and wear) were in use simultaneously. Since the tips of feather barbs in the light bars wear more rapidly than those in the dark bars, older rectrices developed a characteristic pattern of scalloping along their margins. This was particularly evident with the central pair, which cover the other rectrices whenever the tail is folded (i.e., most of the time since birds are usually on the ground foraging, resting, etc.) and thus receive the full effect of tropical sunlight. Some rectrix molt probably occurs on the breeding grounds before southward migration since a few unfaded, recently acquired rectrices were seen among adults in the early fall.

Johnston and McFarlane (1967) found that sex in adult Lesser Golden-Plovers could be determined from the color and pattern of the sixth rectrix. They stated (p. 160): "in males this feather is usually barred black and white, whereas in females it is virtually unbarred and gray-brown. There is considerable individual variation in these patterns, however; in a few males (proven by dissection) the outer rectrices were unbarred and gray-brown and some females even had these feathers more or less barred like the usual male pattern." Saito and Walker (1972) further described dimorphism in the sixth rectrix and found it to be about 80% accurate as a sex criterion in a sample of 38 collected birds. Kinsky and Yaldwyn (1981) reported that male and female sixth rectrices are so distinct that even variations about the norm can be accurately recognized; however, our findings do not substantiate this.

The 57 adults collected at BAFS consisted of 27 males and 30 females, and from this representative sample, the general appearance of the sixth rectrix in adults can be described as follows: (1) *Typical males* (Fig. 6d) had dark gray-grayish white (essentially black-white in a new feather) barring crisply defined across most of the feather. The number of bars varied among individuals. In some birds the bars were about equal in width, in others the dark bars were wider than the white. (2) *Typical females* (Fig. 6e) had more somber coloration of the sixth rectrix with the barring brownish gray-grayish white. The grayish white bars were less sharply defined, often poorly developed, and usually extended only partially across the feather. (3) *Atypical individuals* (Fig. 6f, g) were relatively frequent, and in these instances the above features overlapped such that either sex could be misidentified. Kinsky and Yaldwyn (1981) indicated that variant males and females can still be distinguished since males have more evenly spaced bars and dark coloration at the base of each vane, while females always have white coloration at the base of the inner vane. We found these features much too inconsistent to be useful, and concluded that it was impossible to avoid misidentification of sex in some fraction of the birds examined.

In an effort to objectively assess the extent of this problem, we did a blind evaluation of our specimens. A small piece of paper was clipped over each label obscuring the information thereon, a student then handed each specimen (chosen at random) to one of us (O. W. J.) who identified its sex. The results were: 24 males and 23 females correctly identified, 3 males incorrectly called females, and 7 females incorrectly called males. Overall, this was 47 of 57 correct or 82%, which essentially duplicated the results of Saito and Walker (1972). The data suggest that one is more apt to misidentify a female (23 of 30 correct, 77%) than a male (24 of 27 correct, 89%). Fading between molts would cause a male rectrix to resemble the coloration of a female rectrix and hence be a factor in misidentifying males. Whether individual variation in sixth rectrix morphology persists for the life of the bird is unknown. That this feather might become a more reliable indicator of sex as the bird grows older seems reasonable since many of these plovers do not acquire their definitive alternate feathering until the second or third prealternate molt.

We found the juvenal sixth rectrix to be of little use in sex determination. Both sexes can have the typical drab feather and both can show

degrees of barring (Fig. 6a, b). The only notable feature was that the most strongly barred juvenal rectrices usually indicated males (Fig. 6c).

Efforts to find another plumage character indicating sex that could be used instead of, or in addition to, the sixth rectrix were unsuccessful. We scrutinized rump, breast, crown, scapular, and cheek feathers (from adults and juveniles of both sexes collected in the winter and spring at BAFS) without detecting any sexual dimorphism. Thus, the outermost rectrix remains the only known sex criterion throughout most of the year. In the spring and early summer, the sexes are separable by differences in their respective alternate plumages as described earlier.

## AGE DETERMINATION

The general chronology of golden-plover migration in Hawaii has been known for some time, and appears to be remarkably constant from year to year (Dole 1879, Henshaw 1910, Munro 1944, Morita and Walker 1964, Giffin and Medeiros 1968, Johnson et al. 1981). Most adults and first-year migrants return to the wintering grounds in August, juveniles begin arriving in late September; spring migration occurs in late April–early May.

By the time the juveniles arrive, many of the older birds (nearly 50%) are already in basic plumage, the others are in prebasic molt and show varying amounts of alternate plumage. Recognizing the latter birds as older than juveniles obviously presents no difficulty. The juvenal and basic plumages also are distinct despite the confusion of early observers who portrayed these as essentially indistinguishable without the birds in hand (Bent 1929, Witherby et al. 1940). Juveniles can be readily identified through most of the fall and early winter by dark-tipped feathers in the underparts that produce a delicate yet conspicuous pattern of ventral barring (Prater et al. 1977) not present in the basic plumage of older birds. The barring is lost by late November–early December as the juvenal plumage is replaced during the first prebasic molt. Thereafter, age determination requires that the birds be in hand so that the condition of the primaries and the appearance of the sixth rectrices can be evaluated.

Juvenal primaries appear fresh in the fall, undergo gradual wear and fading during the winter, and are worn by spring. The primaries of older birds show variable degrees of wear in the fall and will be in molt, are fresh in midwinter (some still molting), and are unworn to slightly worn by spring. The same age-related contrasts in primary condition were described by Prater et al. (1977). When present, the drab juvenal sixth rectrix is a helpful age criterion. However, the appearance of this feather varies significantly and it can be mistaken for an adult rectrix; also some juvenal individuals molt their sixth rectrices during the first winter and acquire adult-like replacements.

The foregoing features produce a relatively simple system for separating juveniles from older birds in the fall and spring: fall juveniles (September–early December) have barred underparts, fresh primaries, and often drab sixth rectrices; spring juveniles (March–April) have very worn primaries. During the winter (mid-December–February) the separation is less satisfactory because primary wear in some adults is similar to that in juveniles. The adults in this case are presumably "over-summering" individuals which complete primary molt early resulting in noticeable wear by mid-winter. The problem resolves itself as the season progresses since the juvenal primaries wear more rapidly than those of adults and thus become very distinct by spring.

While recognition of juvenal birds is relatively straightforward, age determination in older birds is more complex and possible only in certain situations. Among "over-summering" plovers, two age-groups are readily separable as follows: first-year birds have very worn juvenal primaries which they begin to molt in June or July, body plumages vary from basic to partial alternate, and usually the cloacal bursa (though reduced in size) is present; 21-month old adults have slightly worn primaries (acquired during the molt just mentioned) which they start molting in June or July, usually well-developed alternate plumages, and no cloacal bursae. As the season advances, fall migrants with different degrees of primary wear join the "over-summering" birds. Of the returning migrants only those with very worn juvenal primaries can be accurately identified as first-year birds. Other individuals with moderate or slight primary wear cannot be assigned a specific age. We can only conclude that these represent birds that either did (moderate wear) or did not (slight wear) "over-summer" in the previous calendar year. Figure 4 is a schematic of the patterns that most reasonably account for the variations we found in Hawaii and at Enewetak, and for those described elsewhere by other investigators (Stresemann and Stresemann 1966, Kinsky and Yaldwyn 1981). We emphasize that this diagram probably could not have been derived without concurrent collecting and banding over the entire wintering season of 1979–1980. This approach enabled us to check age criteria based upon plumage against specimens where young birds could be positively identified from the

morphology of the cloacal bursa and reproductive organs. We found the bursa, which has a life-span of about one year in this plover, to be particularly helpful in formulating our concepts of the molt cycle.

## "OVER-SUMMERING" IN THE PACIFIC

The biology of plovers "over-summering" at Enewetak Atoll was documented by Johnson (1977, 1979). Based upon the information shown in Figure 4, certain conclusions from these earlier studies must now be revised. Using specimens collected during two visits to Enewetak (9 June–6 July 1970, 4–17 July 1973) Johnson proposed that "over-summering" first-year birds had molted their juvenal primaries during the prebasic I molt in the previous winter. "Over-summering" plovers at Enewetak were found in various combinations of basic plumage, degrees of alternate plumage, very worn primaries, and slightly worn primaries. Johnson felt that these were all first-year birds and that variable primary wear could occur if individuals flew variable distances subsequent to the prebasic I molt (i.e., slightly worn primaries had the least use and vice versa). As discussed earlier, and shown in Figure 4, no such molt of juvenal primaries occurred in Hawaii. In fact, the 13 first-year plovers collected at BAFS in the spring (Table 2) all had worn, faded juvenal primaries totally unlike the fresh primaries of adults. Thus, Johnson's earlier conclusion that juvenal plovers molt their primaries in the first winter must be rejected as a misinterpretation.

Present findings indicate that it is much more reasonable to interpret the variability encountered at Enewetak as reflecting an "over-summering" flock composed of first-year birds (very worn primaries, mostly basic body plumage) and 21-month old adults (slightly worn primaries, varying degrees of alternate body plumage; patterns 3 and 4, Fig. 4). Kinsky and Yaldwyn (1981) reached a similar conclusion in their studies of plovers "over-summering" at Niue Island in the southwest Pacific.

While "over-summering" behavior in first-year shorebirds has been known for many years (literature reviews by McNeil 1970, Johnson 1973), the degree of variability which we found for this age group in Hawaii was heretofore unrecognized. In April, first-year specimens varied from basic to full alternate plumage and many were indistinguishable from adults without the birds in hand. Those with better developed alternate plumages migrated (pattern 2, Fig. 4), the others "over-summered" (pattern 3, Fig. 4). With respect to the first northward migration by young birds, it is noteworthy that Sauer (1963) reported spring migratory activity in captive first-year plovers that he had raised from chicks, and Connors (1983) found very worn juvenal primaries among specimens collected on the breeding grounds. We agree with Stresemann and Stresemann (1966) that most "over-summering" birds will become migratory by their second spring (i.e., after about 19 months on the wintering grounds). A few individuals will "over-summer" for a second time (pattern 4, Fig. 4) and migrate in their third spring (i.e., after about 31 months on the wintering grounds).

In their studies at Niue Island, Kinsky and Yaldwyn (1981:23) concluded that "First-year birds remain in their winter quarters for a whole year and most then remain for an additional year and do not return north until April of their third year (thus spending about 31 months in winter quarters)." Our data do not substantiate this long a stay for "most" plovers. Unfortunately, we cannot compare our findings directly with those of Kinsky and Yaldwyn because we have used primary wear and the cloacal bursa as major age indicators while they relied on the juvenal sixth rectrix and the degree of alternate feathering. We have found significant variability in the latter criteria, and in our opinion, Kinsky and Yaldwyn have likely overestimated the length of time spent in "over-summering." On the other hand, if one assumes that "over-summering" reflects the maturation of physiological mechanisms basic to long-distance migration, then it is possible that "over-summering" becomes more prolonged with increasing distance from the breeding grounds. This possibility is supported by the relative scarcity of "over-summering" plovers in the Hawaiian Islands (where they have never been reported in large numbers; we saw only a few at BAFS and KMCAS) as compared to their relative abundance at Enewetak (Carpenter et al. 1968, Johnson 1979). If such a pattern does occur in the Lesser Golden-Plover, it would seem reasonable to expect the major adjustment to occur among first-year birds such that fewer would migrate northward, and that this in turn would result in most birds undertaking their first northward migration in their second spring (i.e., as 21-month old adults, of which about 19 months were spent on the wintering grounds). These details await clarification through investigations on the southern reaches of the winter range. Such studies must employ the full complement of age indicators and, ideally, should include marked birds. Also, the timing of observations is critical. Kinsky and Yaldwyn (1981) saw "250–300" plovers at Niue Island during the period 21 August–1 September 1972, and concluded that these were "over-summering"

birds. Fall arrivals on our study sites in Hawaii (migrants appearing in early August, many birds by mid-August) indicate that Kinsky and Yaldwyn's observations were made too late in the season to rule out the presence of migrants.

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