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MOLT OF WINTERING LEAST SANDPIPERS[1]

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Little information is currently available on the annual cycle of the Least Sandpiper (*Calidris minutilla*). In fact, information on the annual cycle of most shorebirds is limited largely to their breeding biology, and few detailed accounts exist on the biology of shorebirds on the wintering grounds. Between 1971 and 1973 I studied the occurrence, age and sex composition, and molt of Least Sandpipers on a California wintering area. Data were also collected during the study to determine how molt is timed to coincide with feeding conditions on the wintering grounds.

METHODS

The study was conducted from June 1971 to June 1973 on Bolinas Lagoon, a shallow 570-hectare estuary 24 km north of San Francisco, California. Except for two occasions all shorebirds on Bolinas Lagoon were censused once during every five-day period from 5 June 1971 to 4 June 1972. The estuary was divided into three areas and the birds were counted or estimated simultaneously by an observer in each area. On some censuses some of the small sandpipers (Least Sandpipers, Dunlins (*Calidris alpina*), and Western Sandpipers (*Calidris mauri*)) could not be differentiated. These birds always made up less than 20% of the small sandpipers that were identified and were incorporated into the census totals as Least Sandpipers, Dunlins, and Western Sandpipers according to the relative abundance of these species on the census. Most censuses were taken on flood or ebb tides 1.1 m to 1.7 m above mean low water.

I trapped birds night and day in mist nets over mud flats or over pools and channels in salt marsh (*Salicornia virginica, Spartina foliosa, Distichlis spicata*). Bill lengths, measured to 0.1 mm, were used to infer the sex of trapped birds as outlined below. Birds less than one year old had buffy edges on their lesser and middle upper wing coverts or on the tertials whereas birds more than one year old lacked buffy edges on these feathers (Page and Bradstreet, 1968). Although it is not known at what age most Least Sandpipers first breed, in this paper "adult" refers to birds more than one year old and "immature" to birds less than one year old.

Molt was recorded for six body regions: crown, upper back, rump, throat, breast, and abdomen. I estimated the number of growing feathers (pin feathers and feathers with sheaths) for each body region and scored the molt from 0 to 3 as shown in Table 1. The

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TABLE 1

Molt score for six body regions from the estimated numbers of growing feathers in each region.

Molt score	Number of growing feathers					
	Crown[a]	Upper back[b]	Rump	Throat	Breast	Abdomen
0	0	0	0	0	0	0
.5	1	1	1	1	1	1
1	2–8	2–6	2–4	2–8	2–6	2–8
2	9–15	7–11	5–8	9–15	7–11	9–15
3	16+	12+	9+	16+	12+	16+

[a]Includes frontal and coronal regions.

[b]Includes interscapular region as depicted by Holmes (1966a).

molt score for the entire body is the sum of the different body regions. On each wing I grouped the feathers into 10 primaries, ignoring the vestigal 11th, 10 secondaries, and 5 tertials. I included as a tertial the small innermost feather that Holmes (1966a) apparently did not consider a tertial in the Dunlin.

Various methods have been used to collect and analyze molt data in other studies of shorebirds. Therefore, to compare the duration of the prebasic molt of the Least Sandpiper with other shorebird studies I adopted a general method. Beginning at the date the first bird was found with growing primaries, the period of flight feather replacement for an individual was considered to extend to the date the first bird was found with all new primaries; the period of initiation of flight feather replacement for a population extended to the date the last bird was found with all old primaries; and the period of flight feather replacement for a population extended to the date the last bird was found with growing primaries. Dates for these events were taken from the text or extrapolated from the figures in Holmes (1966a, 1971) and Thomas and Dartnall (1971a, b).

Birds were color-marked with colored plastic tape over two aluminum leg bands. The color of one band on the tarso-metatarsus indicated the location of banding and two colors on the other band, the sex of the bird and the season of banding. The position of the dual-colored band, on the right or left tibiotarsus, indicated the age of the bird. Many censuses were taken with a 20 X spotting scope to record the colors of marked birds and the numbers of marked and unmarked birds on the estuary. These censuses were taken over wide areas to reduce any bias that might be introduced by a tendency for individuals to be restricted to a small portion of the estuary.

I estimated the proportion of Least Sandpipers, marked between July 1971 and April 1972, that returned to Bolinas Lagoon the following season. The number of marked birds that returned was determined for three separate periods between August and mid-

September by multiplying the proportion of marked birds by the total number of birds on the estuary. The proportion of returning Least Sandpipers was estimated from the number of marked birds that returned divided by the total number of birds marked the previous season.

Potential food resources for the Least Sandpiper were measured in a 280 m X 20 m plot from June 1972 to June 1973. Cores were taken of the sandy substrate in jars with an inside diameter of 4.8 cm and a depth of 11.5 cm. They were collected bimonthly at 10 m intervals along the length of the plot giving 56 cores per month. Cores were washed through a sieve with 1 mm mesh and the trapped organisms were identified and tallied. Algae (*Enteromorpha* sp.) that grows on the plot was collected occasionally, and invertebrates were washed from it into the 1 mm opening sieve, identified, and tallied. The amount of algae in the plot was estimated monthly as the area of the plot covered by the algae.

SEX OF LEAST SANDPIPERS

I examined 89 Least Sandpipers (museum specimens) collected between 15 March and 15 June 1885 to 1962, in California, British Columbia, and Alaska. To decrease the probability of including incorrectly sexed museum specimens, only birds in breeding plumage were used. Bill measurements (from the tip to the point where the feathers meet the upper mandible) of 43 males had a range of 16.0-18.5 mm, a mean of 17.0 mm, and a standard deviation of 0.5 mm. Bill lengths of 46 females ranged between 17.2-20.2 mm, had a mean of 18.7 mm, and a standard deviation of 0.8 mm. These measurements are similar to those obtained by Jehl (1970) for breeding Least Sandpipers at Churchill, Manitoba—bill lengths of 41 males ranged from 15.8-18.6 mm with a mean of 17.4 mm, and the bill lengths of 41 females ranged from 17.6-21.0 mm with a mean of 18.9 mm.

For color-marking purposes Least Sandpipers with bill lengths $\leq$17.4 mm were considered to be males and $\geq$ 18.7 mm, females. In the 89 west coast specimens examined, 88% of the males and 2% of the females had bill lengths $\leq$ 17.4 mm and 46% of the females and none of the males had bill lengths $\geq$ 18.7 mm. The sex composition of marked birds was compared with that of the birds marked up to the time of observation to reveal changes in the sex composition of Least Sandpipers on the estuary. Birds of unknown sex (bill lengths 17.5-18.6 mm) were excluded from all calculations of sex ratios. During the entire period that marked birds were censused, females made up 44-49% of the adults and 56-57% of the immatures that had been marked.

OCCURRENCE ON THE WINTERING GROUNDS

In 1971 adult Least Sandpipers appeared on Bolinas Lagoon in early July (Fig. 1) after an absence of about 50 days. That year I was unable to determine when males and females arrived; however, in July 1972, by looking for birds marked the previous season, I found the first returning birds were mostly females. In fact until

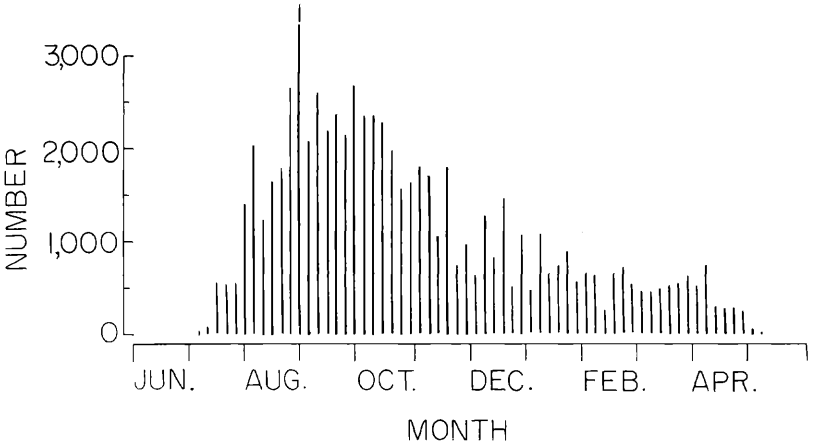

FIGURE 1. Number of Least Sandpipers on Bolinas Lagoon from July 1971 to May 1972.

the second week of August females made up a higher proportion of the marked birds than expected if both sexes had returned simultaneously (Fig. 2). Birds marked as immatures the previous season and now in their second year arrived slightly later than older birds. The appearance of the adult females at Bolinas Lagoon before the males suggests that males have a greater parental role during the fledging period, and consequently remain on the breeding grounds longer than the females. Jehl (pers. comm.) found that female Least Sandpipers at Churchill, Manitoba leave the young very early in the care of the males. No comparable information is available for breeding Least Sandpipers in western North America.

The arrival of post-nesting adults on Bolinas Lagoon before the immatures is typical of many shorebirds including the Least Sandpiper. In 1971, immatures were not observed until the second week of August but by the third week of August they made up 24% of the Least Sandpipers on the estuary. By late August it was difficult to separate the two age classes in the field because some immatures and most adults were in heavy molt. Since immatures were more easily trapped than adults I could not use the age ratios of trapped birds as an estimate for the estuary's population and after August I was uncertain of the age composition of Least Sandpipers on Bolinas Lagoon.

Least Sandpipers were at peak numbers (about 2,400 birds) from late August until mid-October, declined from mid-October to late January, stabilized between 500 and 700 birds until mid-April, then declined until the last birds left in May (Fig. 1). A slight increase in the number of birds appeared in late March and early April (Fig. 1) but since there was no accompanying change in the ratio of marked to unmarked birds, the apparent increase may have been caused by census errors or may have involved marked birds that were returning to Bolinas Lagoon. Also in late March and early

April the proportion of marked females rose sharply (Fig. 2) indicating that males departed from the estuary before females. This suggests that males may arrive on the breeding grounds before the females but this point needs verification from studies of breeding birds. Jehl (pers. comm.) found that male Least Sandpipers arrived on the breeding grounds at Churchill, Manitoba only about one day before the females.

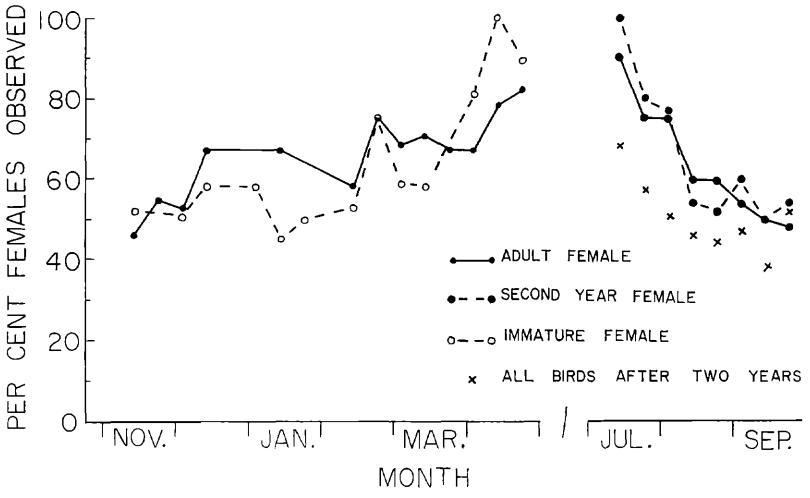

FIGURE 2. Percent female Least Sandpipers in marked birds observed on Bolinas Lagoon from November 1971 to September 1972. Minimum sample size for any point is 10 birds. Adults made up 41% of the marked birds. "All birds after two years" refers to birds marked as adults between July 1971 and April 1972.

Many birds banded on Bolinas Lagoon between July 1971 and May 1972 returned the following season. Between late August and mid-September 1972 from 22.4-29.9% (mean 25.9) of the adults and 19.6-25.5% (mean 22.3) of the immatures marked between July 1971 and May 1972 were back on Bolinas Lagoon. The return rate for both sexes was similar, averaging 25.5% for the males and 24.0% for the famales. In the period of marking, July 1971 to May 1972, there were 35 sightings of marked Least Sandpipers at other locations between 7 km and 21 km from Bolinas Lagoon and seven additional sightings during the period in which return rates were being calculated. Return rates were calculated when Least Sandpipers were at maximum abundance on the estuary but some birds may have returned at other times and left without being counted.

MOLT

Definitive Prebasic (Postnuptial) Molt

Adult Least Sandpipers underwent a complete molt in the late summer and early autumn. Although some adult Least Sandpipers

shortly after their return to Bolinas Lagoon in early July were already molting body feathers, high molt scores were not characteristic of the estuary's population until late July (Fig. 3). The few birds in late August with low molt scores were probably late arrivals or individuals in transit to other molting areas. The start of body molt preceded flight feather molt by an undetermined period because body molt had probably begun in most birds before they reached the estuary.

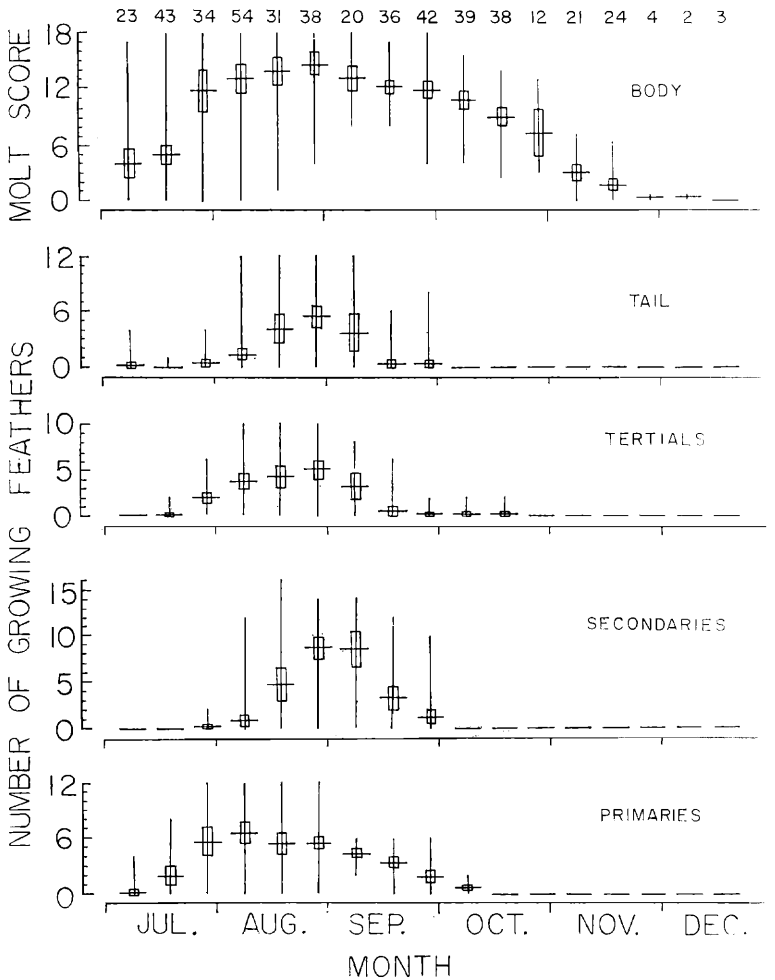

FIGURE 3. Intensity of adult prebasic (postnuptial) molt in Least Sandpipers on Bolinas Lagoon. Vertical line is range, horizontal line is mean, and rectangle is the 95% confidence interval of the mean. Sample size is indicated at the top of the figure.

A few adults were replacing flight feathers in early July but most did not begin flight feather replacement until late July (Fig. 3). The sequence of primary and secondary replacement was similar to that reported for the Red-necked Stint (*Calidris ruficollis*) by Thomas and Dartnall (1971a). Tertial replacement began at the innermost feather and progressed outward until all tertials were replaced. Tail molt started at about the same time as the secondaries and sometimes proceeded from the innermost to the outermost feathers. However, as Thomas and Dartnall (1971a) reported for the Red-necked Stint, molt of the rectrices was far less regular than molt of the remiges and in many Least Sandpipers the "normal" sequence was not followed. There was also a greater tendency for variation in replacement of rectrices on opposite sides of the tail than in replacement of remiges on opposite wings.

Flight feather molt reached peak intensity between early August and mid-September (Fig. 3) and was complete by mid-October. Body molt also reached peak intensity during the same period but tapered off more gradually than flight feather molt and was not complete until late November (Fig. 3). The prebasic molt lasted about 145 days in the Least Sandpiper population on Bolinas Lagoon and the replacement of flight feathers about 96 days (Fig. 3). In some individuals the prebasic molt was probably completed in 130 days on Bolinas Lagoon and flight feather replacement in 72 days (Fig. 3).

First Prebasic (Postjuvenal) Molt

Immature Least Sandpipers underwent a partial molt in the autumn that included the body feathers and a variable number of wing coverts, tertials, and rectrices. Replacement of tertials and rectrices varied individually from birds that replaced none of these feathers to others that replaced nearly all of them. The first prebasic molt began in early August, reached maximum intensity between mid-September and mid-October, and was completed by the end of November (Fig. 4).

Prealternate (Prenuptial) Molt

Adult and immature Least Sandpipers on Bolinas Lagoon in the spring underwent a partial molt that included most body feathers, some wing coverts, some tertials, and some rectrices. There were no differences in the timing or extent of this molt between the two age classes. Considerable individual variation was found in the number of tertials and rectrices replaced and often in the position of the replaced feathers on opposite sides of the wing and tail. The prealternate molt began in mid-February, reached peak intensity between mid-March and mid-April, and was of low intensity in the last birds that were trapped at the end of April (Fig. 5).

FEEDING CONDITIONS DURING THE ADULT PREBASIC MOLT

Limited data on the feeding ecology of Least Sandpipers at Bolinas Lagoon suggest that the adult prebasic molt occurs during optimal feeding conditions. Amphipods (mostly or entirely *Allor-*

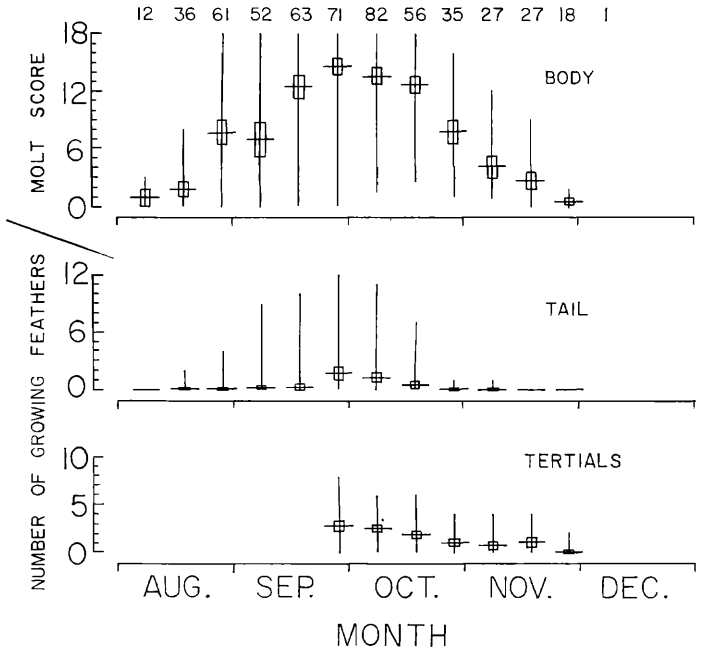

FIGURE 4. Intensity of first prebasic (postjuvenal) molt in the Least Sandpiper on Bolinas Lagoon. Symbols as in Fig. 3.

chestes angustus), which were one of three main prey items in 10 Least Sandpiper stomachs examined (27% of the number of prey items in the stomachs), live in algae (*Enteromorpha* sp.) that have a seasonal cycle of abundance. In July, algae covered 50% of the invertebrate study plot, in August 30%, in September 8%, and in October 3%, but from November to February the area covered was insignificant. Shrinkage of this amphipod habitat and a suspected concomitant decline of amphipod numbers occurred throughout the estuary. Other amphipods (*Corophium* spp.) were also major prey (23%) of Least Sandpipers but lived in the sandy substrate rather than in algae. In July and August *Corophium* spp. (mean 5.3 per core) were more than twice as abundant as between September and February (mean 1.9 per core). Small gastropods (*Lacuna* sp. and *Phytia* sp.) were the third major prey item found in the stomachs (36%) but they were eaten primarily by one bird (98% of the gastropods were found in one stomach) and did not occur in the study plot.

Evidence of a winter decline in potential food resources for shorebirds at another California estuary is provided in studies of the seasonal abundance of invertebrates in a mud flat at Humboldt Bay by Carrin (1973). Carrin found that in the upper 10 cm of the substrate overall numbers of invertebrates were lowest between November and February and the biomass of all invertebrates com-

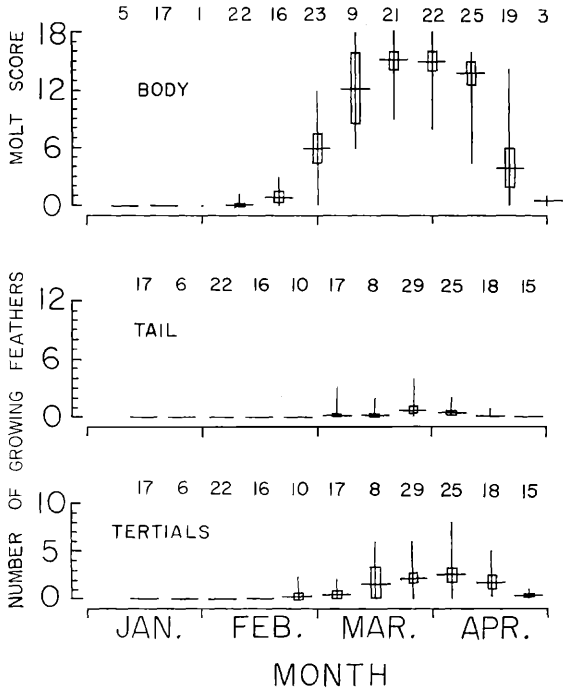

FIGURE 5. Intensity of prealternate (prenuptial) molt in the Least Sandpiper on Bolinas Lagoon. Symbols as in Fig. 3.

bined was lower between November and May than during the remainder of the year. Amphipods, including *Allorchestes angustus* and *Corophium ascherusicum,* were at maximum abundance from July to August and at minimum abundance from November to April.

At Bolinas, most of the Least Sandpipers' prebasic molt is completed in both age groups before the end of October when rain and high tides periodically combine to create unfavorable feeding conditions on the estuary. During the study rain and high tides, occurring simultaneously on several occasions, resulted in prolonged flooding of the mud and sand flats. On these occasions birds were forced into the salt marsh or pastures adjoining the estuary. Since most birds abandoned these areas when the flats were uncovered, apparently the flooding deprived the birds of a preferred feeding area. After October feeding conditions on the estuary may also deteriorate because mud and sand flats are sometimes covered for prolonged periods during rainy weather.

After most of the prebasic molt is complete many Least Sandpipers leave Bolinas Lagoon between mid-October and January (Fig. 1) when feeding conditions on the estuary have deteriorated. In 1971-72 only about 25% of the birds on the estuary during the

height of the prebasic molt between mid-August and mid-October remained until spring migration in April.

DISCUSSION

Among five species of *Calidris* sandpipers studied at different locations the adult prebasic molt differs in the time required for primary replacement in an individual, the period required for initiation of primary replacement in a population, and the time required for primary replacement in a population (Table 2). In general the time taken for primary replacement in species that molt at northerly latitudes is shorter than in species that molt farther south (Table 2). The total period for body molt is difficult to ascertain since most birds complete it at a different place from the point of initiation.

Holmes (1966a, 1966b, 1971) discussed replacement of the flight feathers during the prebasic molt of the Dunlin and stressed the relationship of this molt to the Dunlin's breeding cycle and to the environmental conditions on the breeding grounds. He pointed out that in Dunlins in northern Alaska molt is compressed into the short summer season and overlapped with the breeding effort. In southern and western Alaska with a longer snow-free season, molt in Dunlins does not overlap with the breeding effort. In contrast to the Dunlin, other *Calidris* sandpipers breeding in Alaska migrate south before molting. Holmes (1972) suggests that most *Calidris* sandpipers depart from arctic breeding areas before mid- and late summer food shortages occur. He believes the Dunlin is able to remain in the north and molt because the close proximity of its north temperate winter quarters to the breeding grounds permits it to utilize late summer food resources in the Arctic in the absence of potentially competing species. The Western Sandpiper also breeds in close proximity to its north temperate winter quarters but, in contrast to the Dunlin, moves south before it molts due to decreases in the abundance of insect prey near the nesting area and the lack of alternative prey along the Bering Sea coast.

Holmes (1972) argued that for the Dunlin the timing of the prebasic molt is adapted to take advantage of favorable conditions on the Dunlin's arctic breeding grounds. Species that acquire their basic plumage after migration from the breeding grounds must likewise time their prebasic molt in relation to conditions on their migrating or wintering grounds. This appears to be the case in the Least Sandpiper which completes most of its prebasic molt under the most favorable feeding conditions at Bolinas Lagoon.

Other *Calidris* sandpipers such as the Red-necked Stint, the Little Stint (*Calidris minuta*), and the Curlew Sandpiper (*C. ferruginea*) migrate south of the equator before replacing their flight feathers and molt them over a much longer period than either the Dunlin or the Least Sandpiper (Table 2). Indeed, molt is so protracted in the stints and the Curlew Sandpiper that birds appear to be molting during their entire stay on the wintering grounds (Middlemiss, 1961; Thomas and Dartnall, 1971a, b). I can only surmise that environmental conditions on the wintering grounds of the stints and the Curlew Sandpiper in contrast to those on the wintering grounds of

TABLE 2.
Duration of flight feather replacement in *Calidris* sandpipers.[a]

Species and location	Dates of primary replacement				Estimated minimum period of primary replacement (days)		
	First with growing	Last with all old	First with all new	Last with growing	For an individual	Population initiation	For the population
C. alpina Alaska (71 °N)	14 June	24 June	(15 Aug.)	(23 Aug.)	63	11	71
C. alpina Alaska (61 °N)	27 June	23 July	23 Aug.		58	27	
C. minutilla California (38 °N)	7 July	27 Aug.	16 Sept.	10 Oct.	72	52	96
C. minuta S.Africa (34 °S)	(3 Nov.)			(10 Apr.)			159
C. ruficollis Tasmania (43 °S)	(11 Sept.)	(26 Nov.)	(13 Dec.)	(17 Mar.)	94	77	188
C. ferruginea Tasmania (43 °S)	(9 Sept.)	(26 Nov.)	(31 Dec.)	(11 Feb.)	114	79	156

[a]Data from Holmes (1966a, 1971), Middlemiss (1961), Thomas and Dartnall (1971a, b), and this study. Dates in parentheses have been approximated from figures in the above publications.

the Least Sandpiper are relatively uniform and allow the birds to have a protracted molt.

McNeil (1970) examined the molt of Least Sandpipers wintering in northeastern Venezuela and found that the adults are molting when they arrive in early August but are still in breeding or partial breeding plumage. According to McNeil (1970) body feathering is replaced from the beginning of August until mid-September and flight feathers are all replaced in January and February. The prealternate molt lasts from December to April. Since molt in Venezuelan Least Sandpipers differs markedly from molt of those at Bolinas Lagoon, it would be interesting to know how the process in Venezuelan Least Sandpipers coincides with conditions on their wintering grounds.

Pitelka (1959) suggested that an early departure of adult Pectoral Sandpipers (*Calidris melanotos*) from the breeding grounds in July, before the young, may be an adaptation that acts to improve the food situation for the young and hence their survival on the breeding grounds. Apparently adult Least Sandpipers also leave the breeding grounds early since they arrive at Bolinas Lagoon in July, 30 to 40 days before the immatures. Another possible incentive for the early departure of adult Least Sandpipers from the breeding grounds is the advantage to the adults of arriving on the wintering grounds in time to complete their prebasic molt before feeding conditions deteriorate. The arrival of Least Sandpipers at Bolinas in time to exploit optimal feeding conditions on the estuary suggests that the early departure of adult Least Sandpipers from the breeding grounds imparts certain advantages to the adults that winter in California as well as to the young.

SUMMARY

After an absence of 50 days, adult Least Sandpipers arrive at Bolinas Lagoon at the beginning of July. Most males arrive later than females. In 1972, at least 25% of the adults returned to the area in which they previously wintered. Shortly after their arrival on Bolinas Lagoon some adults were in heavy prebasic molt but others probably stopped for only a short period before moving to other areas to molt. The prebasic molt of adult Least Sandpipers coincided with optimal feeding conditions at Bolinas. Although some Least Sandpipers remain on the estuary throughout the winter, many others leave at about the time the prebasic molt is being completed or shortly afterwards. Immature Least Sandpipers arrive on the estuary 30 to 40 days later than the adults and undergo a partial prebasic molt in which most flight feathers are retained. Many immatures also leave the estuary when most of their prebasic molt is complete. Adults and immatures that remain on the estuary until spring have an incomplete prealternate molt that excludes most of the flight feathers. In the spring, male Least Sandpipers disappear from Bolinas Lagoon before females, suggesting that the males arrive first on the breeding grounds.

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