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MOVEMENTS AND HABITAT USE BY WINTERING POPULATIONS OF WILLETS AND MARBLED GODWITS

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ABSTRACT.—A study in tidal habitats of South San Francisco Bay, California, of a group of Willets and Marbled Godwits marked for sight recognition of individuals has provided the first data on local and migratory movements of individuals of these species on the wintering grounds. For the local population as a whole, information was also gathered on population numbers, habitat use and behavior in response to tides, seasons and weather.

The local population was found to roost habitually on an island in a salt marsh during high tides and to feed on a nearby tidal mud flat during low tides. Census data from a tidal mud flat plot showed peaks in numbers of Willets (October) and Marbled Godwits (December) and, when compared to peaks observed in other parts of coastal California, suggested a southward movement of both species through the state during the fall and winter.

Observations of tagged Willets and Marbled Godwits showed the following: Individual birds habitually used certain roosts and feeding areas. A very limited amount of exchange occurred between the habitual roosts and feeding areas and other roosts and feeding areas. The usual distance traveled (one-way) between roosts and feeding areas was about 1000 m. Some Willets were independent of the tidal mud flat and habitually used certain small areas of salt marsh. Sightings of marked Marbled Godwits from inland areas indicate the possibility of a migration on a north-northeast heading from Palo Alto to breeding sites in southern Alberta. Sixty-five percent of the Willets and 35% of the Marbled Godwits returned to the study area (presumably after migrating) long before and independent of the fall migration population peaks. The population peaks probably represent a southward movement of juveniles. The mean interval of absence of marked birds from the study area was 117 days for Willets and 140 days for Marbled Godwits resulting, in most instances, in an eight- to nine-month residence on the wintering grounds. The marked birds exhibited a restricted home range and long-term residence in the study area.

Most shorebirds are highly migratory and their presence in California, a major wintering area, is seasonal. Typically, more than two-thirds of the year may be spent on the wintering grounds. In California, the marine littoral zone, including the shores of the open coast, bays, sloughs and marshes, provides the most extensive habitats utilized. The seasonal occurrence, habitat use, behavior and ecological relationships among migrant and wintering waders have been investigated but, in the absence of marked birds, details regarding local and migratory movements are scarce.

Recently some information has been obtained on local movements of small scolopacids because of the relative ease with which they can be captured and color-banded. Larger scolopacids such as the Willet, *Catoptrophorus semipalmatus,* and the Marbled Godwit, *Limosa fedoa,* although common, are rarely captured and previously have never been marked for sight recognition of individuals. Only one investigator (Luther 1968) has examined the local movements of Marbled Godwits by observing flights between feeding grounds and high tide roosts and seasonal fluctuations in their numbers. Although such studies of unmarked birds do yield data on movements, they inevitably neglect exchanges of birds among wintering populations and the seasonally changing proportion of birds present for a period of time versus those moving through.

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Accordingly, the objectives of the present study were to determine local movements and some aspects of the migratory movements of a group of individually tagged Willets and Marbled Godwits, and to gather information on their numbers, habitat use, and behavior in response to tides, seasons and weather.

STUDY AREA

The study was conducted primarily on the west side of the southern section of San Francisco Bay (Fig. 1) within about 6 km of shoreline from the Dumbarton Bridge on the north to the Palo Alto Harbor on the south. This area consists of extensive tidal mud flats, salt marshes, solar evaporating ponds being used in salt production, and salt ponds not in use, in which rain water accumulates. A golf course lies just inland from a small airport adjacent to the main marsh and a flood control basin with variable ponds is located to the south of the harbor area.

Willets and Marbled Godwits obtain most of their food from mud flats available to them periodically. Storer (1951) has described the tidal rhythms of San Francisco Bay. Luther (1968) has described the main times of movements of Marbled Godwits in relation to tidal cycles.

The salt marshes within the study area amount to about 320 ha and were an important part of it. The Palo Alto salt marsh itself is composed of about 200 ha of cord grass (*Spartina foliosa*) which grows at tide levels from +4 to +5.5 ft above mean lower low water. Pickleweed (*Salicornia virginica*) covers about 120 ha and grows above the +5.5-ft level. Salt grass (*Distichlis spicata*), gum plant (*Grindelia cuneifolia*), and salt bush (*Atriplex* spp.) are also common in the upper levels of the marsh.

Salt pond dikes, varying in height and width, serve as retaining walls and often border San Francisco Bay itself. The salt pond dikes north of Cooley Landing and in other parts of San Francisco Bay are of importance to shorebirds where the salt marsh has been destroyed (Luther 1968).

The mouth of San Francisquito Creek and to a lesser extent the mouth of the Palo Alto sewage outfall served as important feeding areas on the mud flat, presumably because of detritus and nutrient enrichment at these points. The Pacific Gas and Electric Company boardwalks, installed for maintaining the power poles which border the bay, provided access for observers to areas of the salt marsh and tidal mud flat. The nearby golf course, adjacent fields and the ponds of the flood-control basin were of occasional importance during the study.

METHODS

More than 200 h were spent by the first author in field observation from November 1972 to May 1974. Data were taken during all seasons, at all times of the tidal cycle, during all weather conditions, and at all times of the day. However, data from only two nights and only five rainy days were obtained due to insufficient light or interference with optical instruments. During the 17-month study, observations made on 147 different days were usually coordinated with the tidal cycle.

The sites of most observations were the Pacific Gas and Electric (PG&E) boardwalk along the bay in Palo Alto and south of Cooley Landing, and the dikes bordering the Palo Alto salt marsh.

Willets and Marbled Godwits were counted on a mud flat census plot (Fig. 1) and at high tide roosts. Peak departure flight times, peak arrival flight times, tide levels, habitat use and weather conditions were recorded.

Tidal mud flat census methods have been reviewed by Storer (1951), Jehl (1963), Recher (1966), and Gerstenberg (1972). Storer (1951) censused a mud flat when the maximum number of shorebirds were feeding and before the birds got too far away from the high tide mark to be identified. He considered that these conditions were met when the tide was one-third to one-half ebbed, finding that as the tide reached its lowest ebb and the birds had obtained sufficient food, they began to fly about on the mud flat and return to high tide roosts. Channing and Craig (1954) censused a 100-acre plot at high water and low water and obtained the average number of birds using the plot at these times. Pugh (1963) censused a 2-mi strip of tidal mud flat within two hours to either side of low tide to obtain the average number of birds per mile. Cogswell (1966) and Cogswell and Lawrence (1965) censused a mud flat plot at various times of the tidal cycle and obtained the average number of birds using the plot under various schedules of tidal fluctuation. Recher (1966) reported that an accurate representation of species composition occurred on the falling phase of a minus or near minus tide after 30 to 60% of the tidal mud flat was exposed.

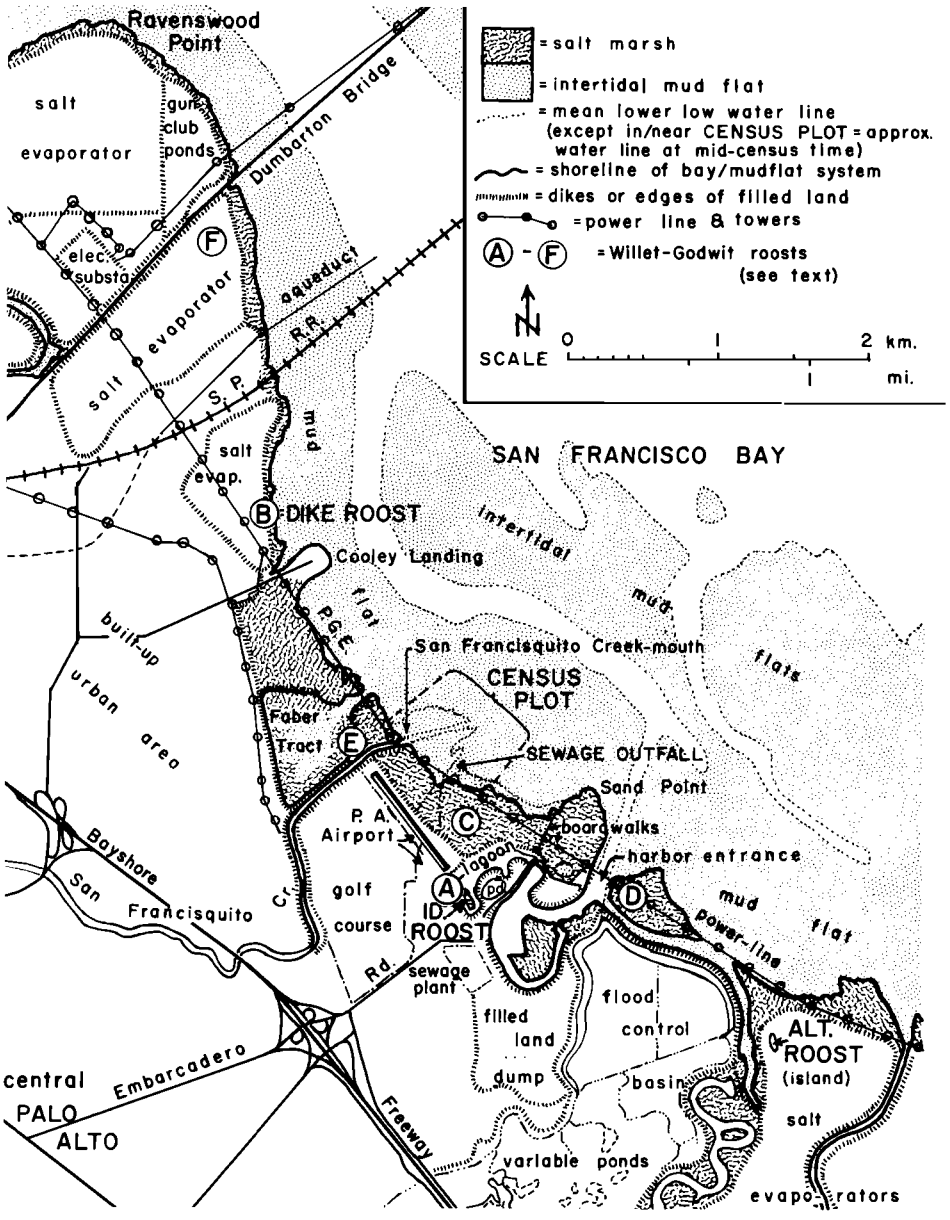

FIGURE 1. Study area on San Francisco Bay.

Using a census plot at the mouth of San Francisquito Creek (Fig. 1), an attempt was made to census Willets and Godwits when one-third of the mud flat was exposed on the ebb phase of a minus or near minus tide (approximately 4 h 45 min after a high tide of about seven feet or more at Palo Alto). At this time there were about 25 ha of exposed mud in the plot. This method usually resulted in the maximum number of Willets and Marbled Godwits within a distance at which they could be identified. However, there are times when falling tides occur only during hours of darkness, and during some periods of the year no minus low tides occur during daylight hours. These factors resulted in time

gaps and sporadic collection of census data at certain times of the year. Obvious landmarks such as permanent wood structures on the mud flat were used to determine tide level during a census. The census plot was scanned with a spotting scope and each Willet and Marbled Godwit seen was recorded. The duration of a census varied during the year from a few minutes to about 30 min.

Counts or careful estimates were made at high tide roosts where birds were usually closely packed. Presence or absence of birds at these high tide roosts, or in any habitat in the study area, was noted.

The majority of field time was devoted to observations of tagged Willets and Marbled Godwits. Ninety-eight birds were captured on 19 February 1973, with a cannon-net at roost A (Fig. 1) using techniques similar to those described by Gerstenberg (1972). The birds were banded, individually marked with patagial tags bearing numbers, and released within six hours. The tags are similar to those used on gulls by Diem (1967), Diem and Condon (1967), and Cogswell (1970, 1974).

Searching for and reading numbers on tagged birds was done mainly in the study area although high tide roosts and mud flats as far away as the Hayward shores, 18.5 km to the north, and the Alviso shores 8 km to the south, were checked occasionally. High tide roosts known to be used by tagged birds were frequently checked and an attempt was made to determine tag numbers with a spotting scope. The tidal mud flat including the census plot was also searched for tagged birds. Tag number, date, time, habitat, and behavior of any marked individual identified were recorded. An individual was only recorded more than once on a given day if it was observed more than about 300 m away from the initial location, or more than one hour after the initial sighting.

Tags were more noticeable on active birds on the mud flat as their movements tended to uncover the numbers on the tags, which were sometimes partially covered by the scapular feathers. In good light on a cool, calm day tags could be seen on birds as far away as 1500 m and a clearly visible number could be read at 800 m. Sleeping or inactive birds were often able to conceal the main part of a tag, thus making numbers difficult to discern. Circulars requesting specific information on observations of tagged birds were posted at various locations in the San Francisco Bay area and mailed to museums, schools, and wildlife management agencies in western North America.

RESULTS AND DISCUSSION

Habitat Use

Within the study area Willets and Marbled Godwits were found to use two high tide roosts (A and B, Fig. 1) consistently, although occasionally one alternate roost (C) was used. Roost A, the usual and most important roost in the Palo Alto area, was on an island in an enclosed lagoon. The island was separated from the mainland by about 5 m at the narrowest channel. Willets, Marbled Godwits, Dowitchers (*Limnodromus* spp.) and to a lesser extent smaller shorebirds would roost on salt grass, pickleweed and areas of bare mud within the vegetation. Difficulty was sometimes encountered in distinguishing between Willets and Marbled Godwits which packed together tightly among the vegetation. The combined numbers of Willets and Marbled Godwits which utilized this roost ranged from 1700 birds in January 1973 to none during May and June 1974. This roost served as the capture site and the site of many subsequent tag sightings.

Occasionally this roost was abandoned in favor of an alternate roost (C) in the Palo Alto salt marsh. This switch could sometimes be explained by a disturbance at the island roost or by an unusually high tide which would force the birds from the island to the higher portions of the salt marsh. On a few occasions, neither the island roost nor the salt marsh roost was utilized. At such times numbers of birds were found in other high areas of the salt marsh.

The other important high tide roost in the area is located on a salt pond dike, 300 m north of Cooley Landing (B, Fig. 1). The dike, composed of dried dredging spoils, borders on San Francisco Bay; thus the birds at this roost were only a few feet from the mud flat as the tide ebbed. The birds favored the top or the side of the dike away from the bay as this was normally the leeward side. The

roost was only censused on occasion as it played a minor role in the behavior of tagged birds. It was first observed on 26 September 1973 when it was used by 340 Willets and 410 Marbled Godwits, and was subsequently censused four times (28 September 1973, 289 Willets and 362 Marbled Godwits; 12 October 1973, 110 Willets and 58 Marbled Godwits; 21 March 1973, 102 Willets and 133 Marbled Godwits).

The salt pond just south of the Dumbarton Bridge (F) was at times used by large numbers of shorebirds. These were usually Willets, Marbled Godwits, and Avocets (*Recurvirostra americana*) as smaller species could not stand in the relatively deep water. The use of this pond was noted from August 1973, through November 1973, and combined numbers of Willets and Marbled Godwits were estimated on 24 August (1600), 12 October (300), and 18 November (3100). Movements between the mud flats in the vicinity of Cooley Landing and this pond were observed on 24 August 1973 when an estimated 1000 birds were observed to make this flight. Use of this salt pond may explain the reduced numbers observed at the island roost from August through December 1973.

Gerstenberg (1972) found that Willets fed in the salt marsh as the tide began to recede, as they did on the present study area. Loose flocks as large as 35 birds were seen foraging in many parts of the marsh prior to and after feeding on the mud flat. On only one occasion, 11 April 1974, were Marbled Godwits observed foraging in a salt marsh, when about ten birds were seen at the mouth of San Francisquito Creek, while other shorebirds fed on the exposed mud flat. The mouth of San Francisquito Creek served as the major feeding grounds for shorebirds in the study area.

Movements in Relation to Tide Cycles and Weather

During an ebb tide at Palo Alto, large shorebirds would normally arrive at the mud flat shortly after mud was exposed. Initially, birds would begin to leave the high tide roosts for the mud flats individually. Later, usually within 15 min, small groups would depart and within one-half hour the majority of the birds would depart. Marbled Godwits were observed to fly from the island roost (A), from the alternate roost in the salt marsh (C), and from the Cooley Landing dike roost (B) to the Palo Alto mud flats, mainly the mouth of San Francisquito Creek (Fig. 1). Mixed flocks of Willets and Marbled Godwits were often observed during these ebb tide flights; however, Willets were seldom seen to come from the Cooley Landing dike roost to the Palo Alto mud flats, and Marbled Godwits tended to be more gregarious. Behaviors exhibited during these flights were similar to those observed by Luther (1968). Marbled Godwits coming to the Palo Alto mud flats from the Cooley Landing dike roost consistently flew a wide path over the water around Cooley Landing rather than taking the shorter path across land. This behavioral trait was noted for many shorebirds when moving to and from tideflat feeding areas on the San Francisco Bay.

Marbled Godwits tended to arrive at the mud flat prior to Willets, and assembled at the water's edge about 200 m southeast of the Palo Alto sewage outfall where mud is exposed early. From this point, the Marbled Godwits would follow the receding water but also move northwest to the mouth of the sewage outfall while being joined by other Marbled Godwits. This movement was interpreted as an attempt to feed into the wind which usually blows out of the northwest and

to reach the sewage outfall which seemed to concentrate shorebirds. Main arrival occurred within 30 min and both Willets and Godwits would forage while moving north to the creek mouth. At this point the birds would forage along the creek mouth or over delta formed by the creek.

At times, tides with small (short) tidal exchanges would occur. These would result in Willets and Marbled Godwits packing together at the mouth of the sewage outfall where the first mud is exposed in the Palo Alto area. On 12 April 1973, 75 Marbled Godwits and 55 Willets were observed waiting there as the ebbing tide had not yet exposed mud following a previously rather high low tide of +2.2 ft. Such tides result in only small areas of mud being exposed and in a shortened feeding period. Luther (1968) has shown that arrival time is dependent on the length of time the mud was exposed during the previous low tide. In addition, strong winds can pile up water and delay the exposure of the mud flat by approximately one-half hour.

During or following periods of rain, both roosts A and C (Fig. 1) were often abandoned in favor of flooded fields and a golf course. On 9 January 1973, 130 Marbled Godwits were observed feeding on the lawn of the Palo Alto golf course following a period of rain. Gerstenberg (1972) observed the same behavior and mentioned that it may have been caused by siltation on the mud flat making regular food items temporarily unavailable, or flooding of uplands making probing easier and causing earthworms and other macro-organisms to rise to the soil surface. On several occasions during very high tides which flooded the roosts, or after rain, or following previously high low tides, few birds could be found in the study area and they were suspected of roosting or foraging in some flooded area such as the Palo Alto flood basin.

Census Data

Census data for the Willet from April 1973 to May 1974 are shown in Figure 2. Reduced numbers due to spring migration are evident in April with a low in the population during May and a return during June. The peak population of 867 birds was recorded on 12 October 1973, with a subsequent decline during the winter and spring to about 300. This was followed by a rapid decline during April 1974 to only five birds on 3 May 1974. Storer (1951) found the migration pattern of the Willet at Alameda-Oakland to be puzzling as a fall peak was found in late September and early October, but the wintering population was considerably lower until March when the species became scarce. Recher (1963) recorded a fall peak at Palo Alto in late October followed by a rapid decline, and spring peak in mid-March with a rapid decline in April. Jehl and Craig (1971) recorded peak numbers at San Diego in August with large numbers also present in February, March and April. Gerstenberg (1972) found that peak fall flights at Humboldt Bay occured in mid-July and late August and spring movement occurred from late March to mid-April. Jurek(1974) tends to confirm these observations. Considering these data with those from the present study, a shift in peak numbers can be observed from northern to southern California, with fall peaks in north in July and August, peaks in central California in September and October, peaks in southern California (disregarding the August peak) from October through November. Large numbers of birds appear to remain in southern California through the winter into the spring. Thus, there appears to be a movement of Willets from

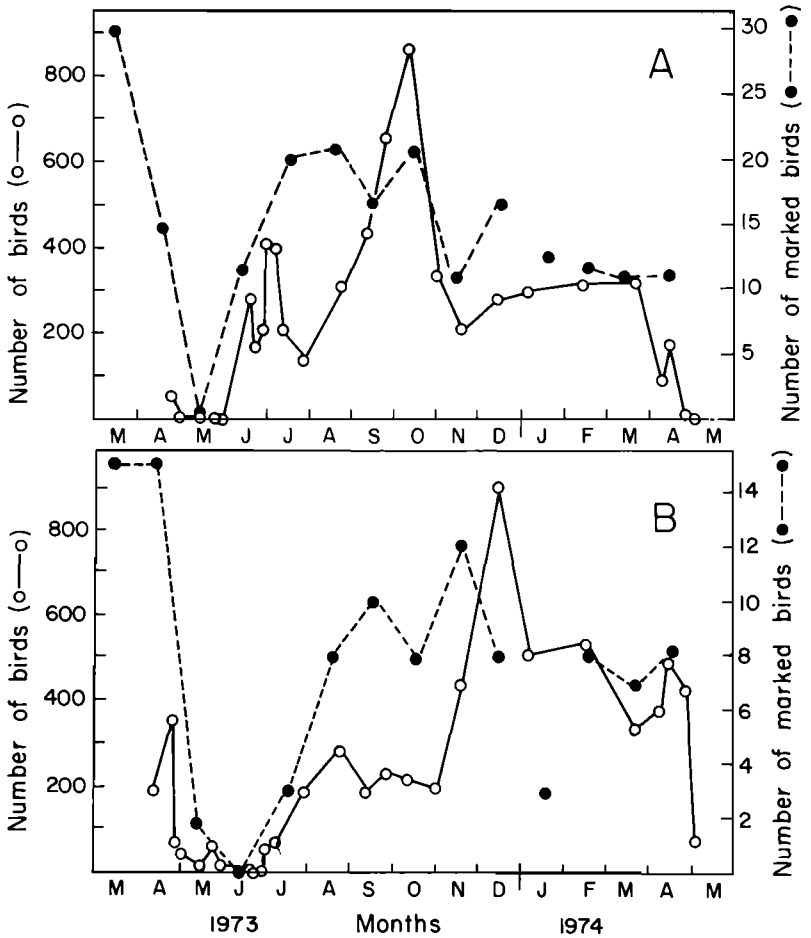

FIGURE 2. Number of birds observed on census plot and number of tagged birds present in the study area March 1973 to May 1974. A, Willet; B, Marbled Godwit.

northern California to southern California through the fall and winter, resulting in the observed fall peak at Palo Alto on 12 October 1973 (Fig. 2), with a subsequent decline in November. No consistent peaks are shown during spring migration but numbers decline rapidly in all parts of the state in April.

The apparent drop in Willet numbers during July and August 1973 (Fig. 2A) illustrates the need to plan census dates carefully as the data obtained in those months are thought to be inaccurate. On 13 July 1973, shorebirds were censused during a very "high" low tide of +3.2 ft following a previous "low" low tide of −0.4 ft. This resulted in a low count, as many Willets did not come to the mud flat to feed. During this low tide many Willets were seen in the salt marsh but an accurate count was not made. A similar situation occurred on 29 August 1973, when the period of censusing fell during a relatively "high" low tide of +3.0 ft following a relatively "low" low tide of −0.7 ft.

Census data for Marbled Godwits (Fig. 2B) show numbers dropping off rapidly during April and reaching a low in June. The numbers of birds increased during

July to about 200 and remained fairly constant until further increases during November led to a peak of 902 birds on 14 December 1973. Numbers then declined rapidly to about 350 to 550 birds, remaining thus until there was a sudden decrease due to spring migration (late April in 1973, early May in 1974).

Storer (1951) observed peak fall flights of Marbled Godwits in September and a peak spring flight in April. Two large peaks reported by Storer (1951) in January and February were doubted by Luther (1968) who indicated that the fluctuations may have been due to the presence of birds in alternate feeding areas not being censused by the investigator. Recher (1966) had incomplete data for the fall migration at Palo Alto but showed spring peaks in April and May. Luther (1968) showed a fall peak at Hayward in December and a spring peak in April. Jehl and Craig (1971) observed high numbers at San Diego in January followed by a slight decline and a peak in April. Gerstenberg (1972) observed fall peaks at Humboldt Bay from August through October with a decline in December, and spring peaks from April to May. Jurek (1974) shows fall peaks in central and southern California from October through January. Excepting Storer's (1951) data, Marbled Godwits tend to show a southward movement in peak numbers through California during the fall and winter. Luther (1968) and the present data show peaks in December, and Jehl and Craig (1971), to the south, show fairly high numbers from January through April. All of the forementioned investigators showed large peaks of Marbled Godwit numbers in April and May while the present study shows only a minor peak in April. During the present study four censuses were made between 21 March 1974 and 26 April 1974; however, one 18-day gap and one 9-day gap may have resulted in the missing of the major peak of the spring migration. Jehl (1968) found that some shorebird movements may be missed if censuses are taken at intervals less than a week.

Luther (1968) found a major departure of Marbled Godwits in late April and the present study similarly demonstrates a rapid decline in their numbers in late April and early May. Gerstenberg (1972), however, mentions a group of 400 Marbled Godwits that was seen summering until late June in the Humboldt Bay area of California, the northernmost coastal bay where they are common. Although it is not unusual to see small numbers of summering Marbled Godwits in the San Francisco Bay area, Gerstenberg's large numbers may, as he mentioned, support Loftin's (1962) findings that some shorebirds migrate north of their wintering range but do not breed and later move south, previous to or with breeders.

Trapping and Tagging

Of the shorebirds captured, 49 were Willets and 45 were Marbled Godwits. There were no mortalities resulting from the capture. Three distressed birds were released untagged. All others were tagged. One bird was found dead and one loose tag was recovered shortly after tagging was conducted. After these known losses, a maximum of 46 Willets and 43 Marbled Godwits presumably remained tagged. Of these, 20 Marbled Godwits (47%) and 17 Willets (37%) presumably left the area immediately as they were not seen again prior to the spring migration. These seemingly premature departures may have been caused by the trapping experience, although some of these birds returned the following fall. These data and the following discussion are based on 567 observations of 40 Willets and 30 Marbled Godwits.

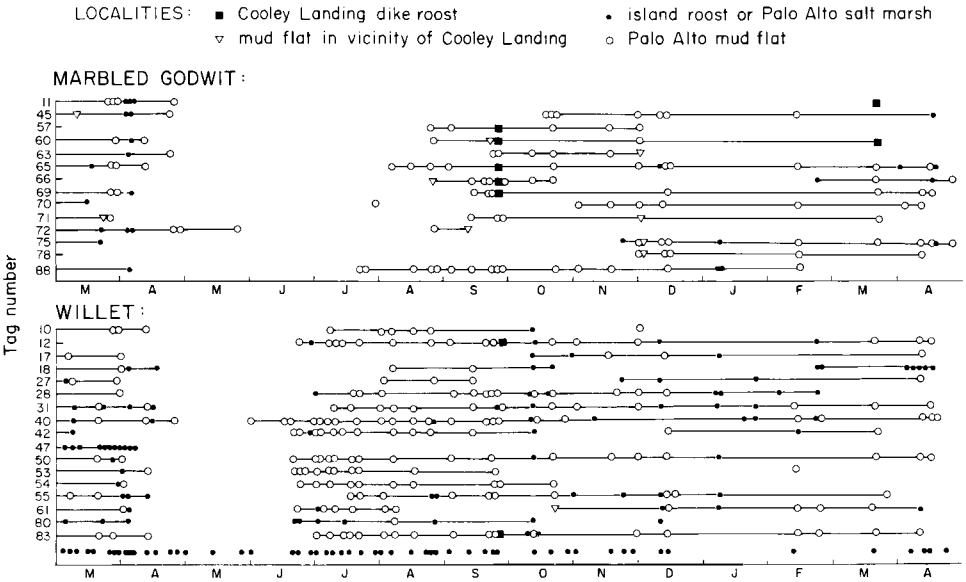

FIGURE 3. Dates and locations of observations of tagged Marbled Godwits and Willets in the study area March 1973 through April 1974. Dots just above the lower horizontal axis indicate dates of searches for tags. Lines connecting plotted points indicate periods of presumed minimal continuous residence in the study area. Willets plotted are those seen nine or more times during the study; Marbled Godwits are those seen seven or more times.

Observation of tagged birds.—Table 1 shows the number of tag observations of Willets and Marbled Godwits made in each section of the study area and the percentages of the total that these observations represent. It is apparent from the data that most tagged birds roosted on the island (A) or adjacent salt marsh (C) and fed at the mouth of the San Francisquito Creek. Figure 3 shows the dates and locations of all observations of tagged Willets seen nine or more times during the study (17 birds), and of tagged Marbled Godwits seen seven or more times (14 birds). Observation of birds not included in these figures were infrequent but otherwise similar to those considered here unless stated otherwise in the following discussion. It can be seen from these data that tagged birds observed repeatedly demonstrated a habitual use of certain roosts and areas on the mud flat. Willet no. 40, for example (Fig. 3), was observed 34 times during 14 months only on the Palo Alto mud flat, in the Palo Alto marsh, and on the island roost.

Marbled Godwits exhibited the same habitual use of certain roosts and feeding areas, but they tended to disperse more than Willets and were found to a greater extent on mud flats north of the mouth of San Francisquito Creek and on the Cooley Landing dike roost. Seven observations of six individual Marbled Godwits were made at this roost (tag numbers 11, 57, 60 (twice), 65, 66, 69; Fig. 3). Two tagged Marbled Godwits (65, 66) returned to the island roost after being seen at the dike roost and one Marbled Godwit (60) was thought to have joined the dike roost permanently (Fig. 3). Willets engaged in this exchange less frequently as only three observations of three individuals (12, 38, 83) were made in the Cooley Landing area and two of these birds (12, 83) were later seen on the island roost

TABLE 1
OBSERVATIONS OF TAGGED BIRDS MADE IN SECTIONS OF THE STUDY AREA

Habitat	Marbled Godwit		Willet	
	N	%	N	%
Roost A	27	14.7	37	9.7
Roost B	7	3.8	3	0.8
Roost C	5	2.7	78	20.4
Mud flat—sewage outfall to Faber Tract	97	52.7	157	40.9
Mud flat—sewage outfall to harbor entrance	24	13.0	95	24.8
Mud flat—Faber Tract to Cooley Landing	7	3.8	2	0.5
Mud flat—Cooley Landing to RR bridge	11	6.0	1	0.3

and in the Palo Alto salt marsh (Fig. 3), Willet no. 38 was not included in Figure 3 since it was observed only six times during the course of the study.

The above observations, however, are exceptions to the usual behavior of most tagged birds already summarized. The latter provide a good indication of the restricted nature of the home range of most individuals of these species on their wintering ground near Palo Alto. The distance from the island roost to the feeding grounds is about 1000 m, a distance much less than the feeding flights of up to 6100 m described by Luther (1968).

It would appear from Table 1 that Willets utilize the salt marsh much more than Marbled Godwits. This is the case but not to the degree indicated by the data. These figures do not provide an absolute measure of habitat use, since the observer's ability to find tags in various habitats varies considerably. Marbled Godwits in the salt marsh and on the island roost packed together tightly, usually slept, and moved little, thus making tag reading difficult. This behavior resulted in a bias in numbers of tag sightings between high tide roosts and on the mud flat (Table 1). In contrast, Willets were often active in the salt marsh and displayed their tags readily. Such behavioral differences were minimized on the mud flat when tags of both species could be read with equal case.

Movements of tagged birds of more than 300 m while feeding on the mud flat were very unusal. Two such movements were observed on 30 November 1973, when tagged Marbled Godwits (numbers 75, 78) moved from the creek mouth to north of Cooley Landing during the same low tide, a distance of 1700 m.

Gerstenberg (1972) describes the frequent use of the salt marsh by Willets but no investigator of salt marsh populations has mentioned the total avoidance of tidal mud flats by some Willets. From 4 March 1973 to 5 April 1973, one tagged Willet was observed 11 times in a small area of the Palo Alto salt marsh during all phases of the tidal cycle and never elsewhere. Another tagged Willet was observed to behave similarly and was observed ten times in a small section of salt marsh from March 1973 to December 1973. It is believed that these birds were not injured or abnormal as the latter bird was eventually seen on the mud flat one-half mile away and other untagged Willets were sometimes seen in the vicinity of these tagged birds. Recher (1963) has described instances of territoriality in shorebirds especially where vegetation is broken up by puddles and mud, as in the section of salt marsh where the tagged Willets foraged, but no instances of aggressive interaction were observed. The possibility remains, however, that the birds were occupying feeding territories.

TABLE 2
MAXIMUM INTERVAL OF ABSENCE FROM STUDY AREA FOR TAGGED BIRDS DURING SUMMER 1973

Willet		Marbled Godwit	
Tag no.	No. of days	Tag no.	No. of days
10	85	45	181
18	110	60	135
24	99	63	154
27	124	65	115
28	89	69	160
31	85	70	133
42	105	71	150
50	84	72	92
53	70	88	115
54	86		
55	95		
61	79		
80	79		
83	78		
Means:	91 days		137 days

Note: Willet no. 40 omitted because bird may have summered. Willet no. 17 and Marbled Godwit no. 75 omitted because it is likely that they were overlooked in early fall 1973.

Two reports of tagged godwits outside the study area were received. One was observed on 6 May 1973, in southwestern Idaho at the junction of the Snake and Boise rivers. The bird was the only one of its species feeding in a field with Willets and American Avocets. The bird flew off when approached and was not seen again. According to the observer, Marbled Godwits are seldom seen in that area. The bird had no prior resighting record in Palo Alto and has never been seen again. It is suspected that the tag may have interfered with flight during migration and caused the bird to separate from its flock. Another godwit was observed on 6 May 1973, in southwestern Alberta, near the town of Indus, 15 mi southeast of Calgary. The bird was in the company of other godwits, which breed in the immediate vicinity. This is the first instance of a banded Marbled Godwit from the wintering grounds being found on the breeding grounds. The bird was able to fly and appeared normal. It was seen three times on the Palo Alto mud flat prior to its departure (last observation 24 April 1973), but not again after the Alberta sighting. The sightings of tagged Marbled Godwits in southwestern Idaho and southwestern Alberta indicate the possibility of a flight path from the wintering grounds on a north-northeast heading to breeding sites in southern Alberta.

Another tagged Marbled Godwit (number 57) was seen for the first time on the Hayward shore of San Francisco Bay 18.5 km north of the study area on 3 August 1973. It was subsequently seen at Palo Alto on 24 August 1973, and on five other occasions through November 1973.

Two Willets were seen outside the study area. The first (number 28) was observed on 26 June 1973, at Bolinas Lagoon 45 mi north-northwest of the study area. This bird was previously seen 19 times beginning 29 June 1973 (three days after it was at Bolinas), and extending to 25 February 1974. The second was found dead on 6 June 1976, near Beckwourth, Plumas County, California, at an elevation of about 1500 m where this species breeds in small numbers. This bird had only been seen once before at Palo Alto, on 25 August 1973.

Fifteen Marbled Godwits, 35% of those originally tagged, and 30 Willets, 65% of those originally tagged, returned to the Palo Alto area after presumably migrating. In view of the faithfulness for the wintering grounds exhibited by the tagged birds, it is thought that most of those that failed to return had probably died.

The interval of absence from the study area during the breeding season was calculated for those tagged Willets and Marbled Godwits for which repeated observations offered evidence of departure and arrival. These data are shown in Table 2. For Marbled Godwits the mean interval of absence was 137 days (N = 9). For Willets it was 91 days (N = 14). The minimum observed interval of absence was 70 days for a Willet, with the exception of number 40 which may have been a nonbreeder. This interval would suffice for a bird that migrated directly to the breeding grounds to then nest and raise young.

Recher (1966), Swinebroad (1964), and Post and Browne (1976) have discussed the length of time that a shorebird spends in an area during migration. Recher (1966) mentions occasional distinctive individuals which were observed over a 1-mo period. He found that those individuals were remarkably constant as to feeding and loafing sites they frequented. He often observed equally distinctive birds that were observed once and then left the area (no dates or species were mentioned). Recher (1966) concluded by examining his own census data and those of Storer (1951) that a shorebird's presence is temporary in any one area on the wintering grounds. As previously mentioned, his data showed population peaks that were interpreted as successive groups of birds moving into and out of an area.

Recher (1966) believed that the influx of migrants into an area would lead to dispersal within and migration out of the area by the former "residents" which would be behaving as a group, due to their similar physiological and psychological levels (thus, the successive waves). This, he believed, would minimize interspecific interactions that might result in competitive exclusion. Until then, the few available returns from banded birds had not clarified the problem. In the Humboldt Bay area, for example, Gerstenberg (1972) recaptured five Marbled Godwits in the fall, 56 days after banding, and one Willet was found dead 75 days after banding.

Our results, however, show that many individual tagged birds were present in the study area for eight to nine months of the year. Nevertheless, Recher's conclusions may apply to some degree. Figure 2 compares the numbers of individual tagged birds observed per month to the total population on the census plot. A decrease in the number of tagged birds in the study area was noted after the winter peaks. However, about two-thirds of the observed maximum number of tagged birds seen after fall return were present after the winter peak. It appears, then, that about one-third of the tagged birds that migrated back may have left the study area for more southerly areas after the winter peaks, while the majority of the tagged birds remained in the study area.

The winter peaks in numbers of Willets (October) and Marbled Godwits (December) on the census plot can be examined in relation to the observed migratory departure and arrival dates for tagged birds (Table 3). The mean arrival dates for tagged birds of both species precedes the winter population peaks by two to three months; and as shown above, the tagged birds were for the most part independent

TABLE 3
MIGRATION DATES FOR TAGGED BIRDS

	Departure			Arrival			Population peak
	N	Mean date	Range	N	Mean date	Range	
Willet	18	6 April	±9 days	27	1 August	±47 days	12 Oct
Marbled Godwit	12	21 April	±13 days	14	13 Sept	±43 days	14 Dec

of the winter peaks and subsequent declines. Bent (1927, 1929) reported that adult Willets and Marbled Godwits leave the breeding grounds before juveniles and this was confirmed for Marbled Godwits by Gerstenberg (1972) when only six birds out of 256 trapped between August 15 and October 11 were in juvenile plumage. These findings may explain the early migration arrival dates of the tagged adults birds and their dependence (for the most part) from a subsequent influx of juveniles comprising the winter peaks observed in October (Willets), and December (Marbled Godwits).

Significance of observations of tagged birds.—Individually marked Marbled Godwits and Willets have provided the first opportunity to examine the habitat preferences and local and migratory movements of individual birds within a wintering population. Marked birds demonstrated a habitual use of roosts in the Palo Alto salt marsh and mud flats at the mouth of San Francisquito Creek. These observations and the few exceptions observed demonstrated the restricted nature of the home range of the tagged individuals.

A comparison of the migration departure and arrival schedules of marked and unmarked birds was revealing. Tagged birds departed along with unmarked birds but arrived considerably earlier than the winter population peaks which probably represent a southward movement of juveniles.

Most of the tagged birds observed were present in the study area for about eight to nine months of the year, and were for the most part independent of winter population peaks. These findings demonstrate that Recher's (1966) general conclusion that a shorebird's presence is temporary in any one area on the wintering grounds is false. Without marked birds, it cannot be assumed that population peaks or waves of the birds moving into and out of an area reflect a turnover in local populations.

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