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Subadult Movement Patterns of the Endangered Hawaiian Stilt (*Himantopus mexicanus knudseni*)

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Data on individual movement patterns are important for understanding foraging patterns, mate acquisition, and dispersal (Baker 1978, Krebs and Inman 1992, Colwell and Oring 1989, Reed et al. 1999). More recently, requirements for conservation biology have resulted in increased interest in the movements of individual (abilities and patterns) because of their relationships to population persistence in fragmented landscapes. Immigration is necessary to maintain local components of metapopulations (Brown and Kodric-Brown 1977), and the parameter that determines the amount of interaction among components of a metapopulation is dispersal (Hansson 1991, Wu et al. 1993).

In this paper, we present data on movements of subadult Hawaiian Stilts (*Himantopus mexicanus knudseni*), an endangered subspecies confined to the main Hawaiian Islands. Most of the data are from the island of Oahu, but we also present information on movements among islands across the range of the subspecies. Hawaiian Stilts forage in shallow water and nest on adjacent flats and embankments (Coleman 1981). Current wetland area in Hawaii is less than 30% of its original extent (Dahl 1990, English and Pratt 1993), and the population size of stilts de-

pends partly on agricultural and aquacultural practices (e.g. runoff from taro, rice, and sugarcane farming) that provide breeding and foraging habitat (Broshers 1979, Griffin et al. 1989). Dependence on agriculture, coupled with habitat conversion for housing and business, has resulted in a fragmented and reduced wetland landscape (Shallenberger 1977, Coleman 1981, Griffin et al. 1989) and disjunct distributions of waterbirds (Reed and Oring 1993, English and Reid 1994, Reed et al. 1994). Hawaiian Stilt population size decreased substantially early in this century until the 1940s (Munro 1944) but increased during the last 50 years (Reed and Oring 1993) to its current population size of around 1,300. Hawaiian Stilts appear to be habitat limited (Reed et al. 1998) and are threatened constantly by exotic predators and exotic wetland plants that make wetlands unsuitable for breeding and foraging (English and Reid 1994). This shorebird study is unusual in that it focuses on short-term, predispersal movements. Although data on shorebird movements exist for some species, they typically focus on dispersal, migration, or foraging (e.g. Oring and Lank 1984, Warnock et al. 1995, Butler et al. 1997).

Study system.—Hawaiian Stilts inhabit seven islands (Hawaii, Kauai, Maui, Molokai, Oahu, Niihau, Lanai), although only the Oahu, Maui, and Kauai

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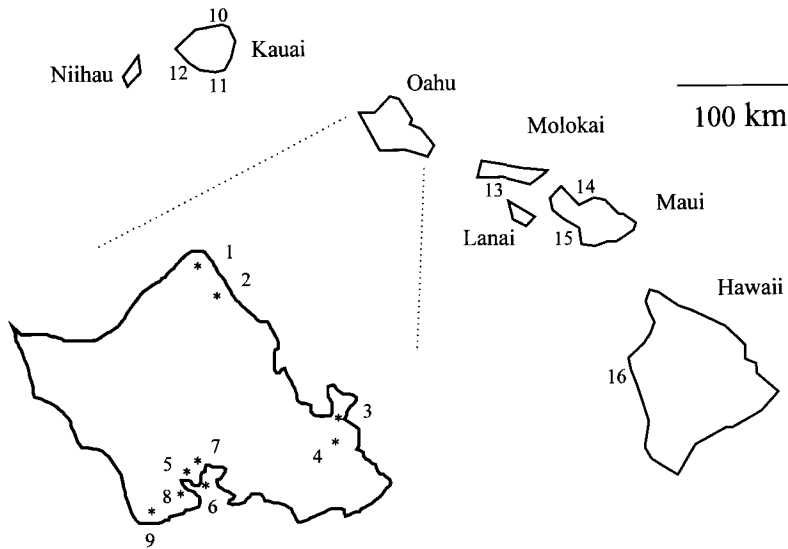


FIG. 1. Wetlands in the Hawaiian Islands where Hawaiian Stilts were banded or surveyed. Oahu is expanded to show detail; numbers correspond to those in Table 1. These and other minor wetlands were surveyed for banded birds. Wetlands are described in Table 1.

populations are large. The presence of stilts on the island of Hawaii might be due to recent recolonization (Paton et al. 1985, Banko 1988) and is the case for their presence on Lanai (Engilis and Pratt 1993). Long-term censuses show that stilt numbers on Hawaii, Molokai, and Lanai historically have been small (<70 birds each; summarized in Reed and Oring 1993), but recent surveys have shown that populations on the Kona coast of Hawaii have increased, and populations on Molokai exceed historic counts (Engilis and McCafferty unpubl. data). Modeling suggests that these smaller populations cannot persist without immigration from islands with larger numbers of stilts (Reed et al. 1998).

Little is known of the spatial structure of Hawaiian Stilts, but birds move among wetlands and among islands (Munro 1944, Telfer 1971, 1972, Pyle 1978, Telfer and Burr 1978, Engilis and Pratt 1993, Reed et al. 1994). Hawaiian Stilts quickly colonize newly created wetlands (Pyle 1978), they use ephemeral wetlands for foraging (Telfer 1971, Broshears 1979), and they move seasonally between Kauai and Niihau (Telfer 1972, 1974, Engilis and Pratt 1993). Limited observations have been made of marked (not individually) birds moving among wetlands and islands (Telfer 1972, Telfer and Burr 1978, 1979).

Methods.—From 1992 to 1995, we banded Hawaiian Stilt chicks (7 to 28 days of age) at wetlands across the state (Fig. 1). Birds were banded from April to July (mostly in June) on all islands except Niihau and Lanai, but most banding occurred on Oahu. Birds were marked with unique combinations of three UV-stable plastic (darvic) colored leg bands

and a U.S. Fish and Wildlife Service aluminum band. All bands were placed on the tibiotarsus.

Oahu wetlands were surveyed weekly for banded stilts from July 1994 through June 1996. Wetlands on Kauai, Maui, Molokai, and Hawaii were surveyed monthly during the same time period. Very few wetlands were inaccessible on these islands; Niihau was not accessible for survey. Because the Niihau birds most likely migrate seasonally to Kauai (Engilis and Pratt 1993), we believe that we adequately surveyed those birds on Kauai during the breeding season. Our surveys were supplemented on Oahu, where additional observations were made regularly on the national wildlife refuges, and by surveying Rowland's Pond most weeks from June 1994 to the end of 1996 (Table 1, Fig. 1). Because Hawaiian Stilts are large and easy to observe (Chang 1990), we believe that surveys were effective at detecting banded birds.

Each banded bird seen was identified and its sex determined when possible (Hawaiian Stilts cannot be sexed using external cues until after their prebasic I molt, and only then in good light; Coleman 1981). We analyzed data for movement patterns by sex, age, and season. Wetlands where birds were banded and surveyed varied in size, complexity, and distance to other wetlands (Table 1, Fig. 1).

Results.—We banded 201 Hawaiian Stilt chicks that were seen at least once after banding (160 on Oahu, 37 on Maui, 2 on Kauai, and 2 on the island of Hawaii). These birds were seen 3,543 times during subsequent surveys. Of these 201 birds, 78 were male, 56 were female, and 67 were of undetermined sex.

Although most banded birds that were resighted

TABLE 1. Primary wetlands surveyed for Hawaiian Stilts. Wetland numbers correspond to those in Figure 1.

Wetland	Number of ponds	Area (ha)
Oahu		
1 James Campbell (NWR), Kii Unit	8 on refuge, ≤120 in adjacent prawn farm	57 on refuge, 30 adjacent (mostly empty after 1995)
2 Kahuku	8	50
3 Kaneohe Marine Corps Air Station, Nuupia Ponds	4	100
3 Enchanted Lake (Kaelepulu Pond)	1	5
4 Pouhala Marsh	1	35
5 Waipio Peninsula Ponds	≤5	15 (drained since 1995)
6 Pearl Harbor NWR, Waiawa Unit	2	8
7 Pearl Harbor NWR, Honouliuli Unit	4	8
8 Rowland's Pond, Chevron Products Co., Hawaii Refinery	1	2
Kauai		
10 Hanalei NWR	4 large, 40 small	16 in large ponds, 10 in small
11 Huleia NWR	1	5
12 Mana Ponds	2	20
Molokai		
13 Kakahaia NWR and Doia-Kaunakakai	1	10 permanent, 200 ephemeral
Maui		
14 Kanaha Pond	6-16	50 permanent, 20 ephemeral
15 Long-Azeka Ponds	2	3
Hawaii		
16 Kona Coast (Opaepula, Aimakapa, Kona sewer treatment plant)	3	50

were not recorded outside their natal wetland (41%), 14 birds were recorded making a total of 31 interisland movements (Fig. 2). Five birds banded on Maui were resighted on Oahu (175 km), three were seen on Molokai (63 km), and two on the island of Hawaii

(138 km). One bird moved between Maui and Molokai 11 times, another moved 10 times, and one bird moved between Maui and Oahu 5 times. One Oahu bird was seen on Maui and two were seen on Hawaii (295 km), and one Hawaii bird was seen on Maui and

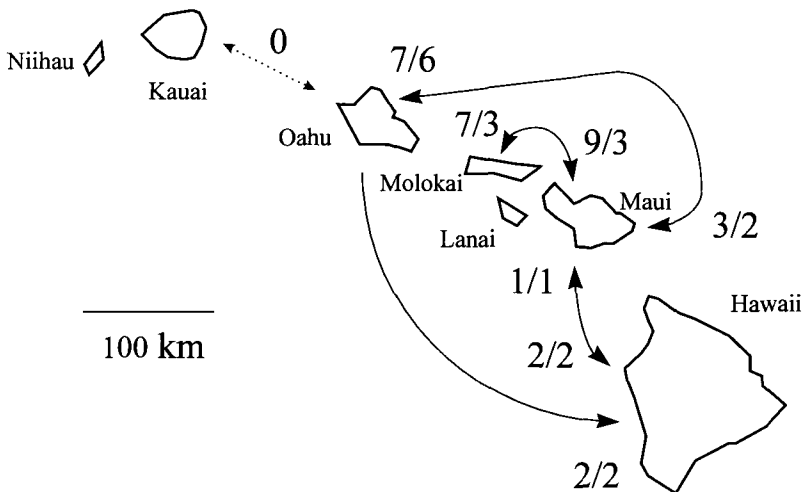


FIG. 2. Interisland movements by Hawaiian Stilts. Shown are number of moves/number of birds making the moves. Numbers by an arrowhead are moves to that island from the arrow's origin.

TABLE 2. Movements of Hawaiian Stilts banded on Oahu and recorded moving among Oahu wetlands (wetland names are given in Table 1). Shown are number of moves/number of birds involved in moves; the leading diagonal is the number of birds that never were recorded outside their natal wetland/number banded and resighted. Distances (km) between wetlands are in parentheses.

	1	2	3	4	5	6	7	8	9
1	40/59	28/12 (0.7)	7/2 (11.7)	0 (13.7)	6/4 (11.0)	2/2 (11.6)	6/4 (11.4)	3/2 (12.1)	7/5 (14.8)
2		0/0	2/1 (11.2)	0 (12.9)	2/2 (10.6)	0 (11.3)	3/2 (11.1)	0 (11.7)	2/2 (14.7)
3			3/6	1/1 (2.0)	1/2 (8.2)	0 (8.9)	0 (11.1)	2/2 (9.9)	1/1 (13.4)
4				0/1	0 (8.5)	0 (9.1)	0 (9.3)	0 (9.8)	0 (13.2)
5					0/0	8/8 (0.8)	24/12 (1.0)	99/38 (1.7)	68/38 (5.4)
6						0/3	0 (0.3)	3/3 (0.9)	9/7 (4.6)
7							2/11	12/9 (0.7)	6/5 (4.5)
8								1/9	66/32 (3.8)
9									15/58

Oahu. These 14 birds were six females, three males, and five of unknown sex. Three siblings moved from Maui to Molokai, and back to Maui; two of these birds (one male, one female) moved together between Maui and Molokai 10 times.

Most of the data on movements among wetlands came from Oahu (Table 2). Of the 59 birds banded at James Campbell National Wildlife Refuge (NWR) and the adjacent prawn-farm ponds (north shore of the island) that were resighted, 40 (68%) were never seen outside of the refuge and surrounding ponds. Birds banded at this wetland were seen at a nearby wetland (0.7 km distant) and in the wetlands in Pearl Harbor region (i.e. southern wetlands; 11 to 15 km), but not at the eastern Oahu wetlands (13 to 14 km; Fig. 1). However, birds banded at the eastern wetlands were seen at the north shore and southern wetlands. Birds banded in the southern ponds moved extensively among the local ponds (0.7 to 5.4 km between wetlands) and to the north and east shores (Table 2). Birds banded in the largest wetlands, which also were the most isolated, were observed moving the least. Overall, the number of moves between pairs of wetlands on Oahu fit a simple function of distance: 175 moves of less than 2 km, 96 from 2 to 5 km, 71 from 5 to 10 km, and 41 from 10 to 15 km.

We looked for movement patterns based on sex, age, and season (breeding [1 April to 31 July] vs. non-breeding). We assumed no difference in detectability between males and females because no behavioral differences that might affect detection are known (Coleman 1981, Chang 1990). These analyses were done on birds banded on Oahu after 1992 (1992 birds were omitted due to excessive human-caused mortality). Females were less likely to move than were males ($\chi^2 = 9.22$, $df = 1$, $P < 0.005$). This relationship varied by age, however. We found no difference between the sexes for hatching-year birds and second-year birds seen before the next breeding season (44% of males and 43% of females moving; $\chi^2 = 0.006$, $df = 1$, $P > 0.50$), but males had a greater tendency to

move as second-year birds during the breeding season (68% of males moved vs. 27% of females; $\chi^2 = 10.97$, $df = 1$, $P < 0.005$). As birds became older, the tendency for females to be more sedentary than males continued; i.e. in second-year birds after the breeding season and in third-year birds before the breeding season ($\chi^2 = 12.98$, $df = 1$, $P < 0.005$), in third-year birds during the breeding season (47% of males moved vs. 11% of females; $\chi^2 = 5.82$, $df = 1$, $P < 0.025$), and in third-year birds after the breeding season ($\chi^2 = 3.35$, $df = 1$, $P < 0.10$). Because of mortality, sample sizes decreased rapidly with age, but cell sizes in the above analyses met statistical criteria for valid testing (Feinberg 1980).

For birds of known sex, the proportion of the resighted birds seen outside their natal wetland decreased with age, from 66% of birds moving between hatching and the next breeding season, to 30% moving as third-year birds during the breeding season. Including birds of unknown sex eliminated this pattern. No patterns were apparent in the proportion of movements during the breeding versus the non-breeding seasons. Birds were highly variable in the cumulative distances that we recorded them moving, ranging from 0 to 736 km (Fig. 3). The mean cumulative distances moved did not differ between the sexes (females, $\bar{x} = 38 \pm SD$ of 118 km; males, $\bar{x} = 26 \pm 62$ km; $t = 0.61$, $n = 113$, unequal variance test, $P > 0.50$, $df = 62.1$). Because birds living longer have the potential to move farther, we repeated this analysis using cumulative distances moved divided by the number of months each bird was recorded alive; the results were unchanged (females, $\bar{x} = 1.9 \pm 6.3$ km; males, $\bar{x} = 1.9 \pm 2.8$ km; $t = 0.91$, $n = 113$, unequal variance test, $P > 0.30$, $df = 57.7$).

Discussion.—Understanding the spatial pattern of wetland use by Hawaiian Stilts is important for understanding population dynamics, developing management plans, and selecting habitat restoration or mitigation sites. One benefit of our study population over most other studies of movement is that we surveyed the entire distribution of the subspecies. Most

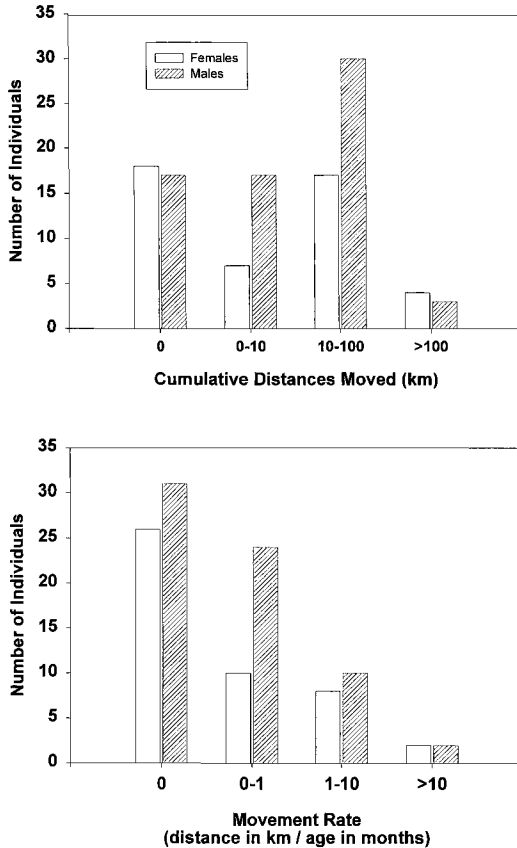


FIG. 3. Cumulative distances moved by male and female Hawaiian Stilts banded on Oahu, and rates of movement. Only banded individuals that were resighted at least once are included, and only movements beyond the natal wetland complex are recorded. Differences between the sexes are not statistically significant ($P > 0.05$).

resightings of banded stilts occurred on the same island (often the same wetland complex) on which they were banded. However, repeated surveys showed that Hawaiian Stilts are capable of extensive movements. Birds banded on Maui made the most moves among islands, possibly because of their centrally located geographic position (Fig. 2). Many of the individuals that made interisland movements moved multiple times. We recorded no movements between Oahu and Kauai, which was one of the few interisland movements previously recorded (Telfer and Burr 1978). However, Kauai is the most isolated of the main Hawaiian Islands, so movement to and from Kauai and the other major islands might be uncommon.

On Oahu, where most birds were banded and the most intensive observations were made, birds moved regularly among wetlands. Frequency of moves de-

creased with increasing distance to the next wetland. We were unable to independently test movement related to wetland size because most banding occurred at one large, relatively isolated wetland and at one small wetland situated near other wetlands. Five wetlands were in close proximity to the small wetland, and birds moved among them frequently. Most individuals banded in the large wetland, including eight ponds of the Kii Unit of the James Campbell NWR, and up to 100 adjacent ponds depending on the status of the prawn-farm ponds, were not recorded outside the wetland. Birds moved extensively among these ponds, but infrequently elsewhere. Movements occurred year-round, and males were more likely than females to move. We hypothesize that this pattern is evidence that males compete for females in this monogamous species and are prospecting for breeding opportunities (Reed et al. 1999). If this pattern reflects dispersal, it is contrary to the female-biased dispersal observed in some monogamous shorebirds (e.g. Jackson 1994). For individuals that moved, there was no difference between males and females in the distance or the rate (distance/time) moved.

Long-distance movement or migration in family groups is common in geese (e.g. Prevett and MacInnes 1980) and Sandhill Cranes (*Grus canadensis*; Tacha 1988) but seldom is reported in shorebirds. For example, Alberico et al. (1992) reported indirect evidence that sibling Spotted Sandpipers (*Actitis macularia*) migrate together. Kitagawa (1988) documented family groups of Black-winged Stilts (*Himantopus himantopus*) moving up to 6 km among wetlands. Because birds were not individually marked, the duration of the association was not known, but some family groups appeared to defend winter territories. Robinson and Oring (1996) found three wintering Black-necked Stilt (*H. m. mexicanus*) siblings 470 km from where they were banded. Although we had several records of siblings moving among islands, we could not determine whether the observed frequency was different from that expected from random movements.

Stilts, in general, are opportunistic breeders that take advantage of wetlands when they are available (Cramp and Simmons 1983). An extreme example of this opportunistic behavior is exhibited by the Banded Stilt (*Himantopus leucocephalus*) in Australia. These colonial nesters breed only on recently flooded salt lakes that form only every few years. After rains begin, these birds migrate from coastal areas to newly flooded lakes in interior regions as far as 1,000 km away and begin breeding almost immediately (Minton et al. 1995). Therefore, stilts are effective colonizers and effective users of ephemeral habitat. This is consistent with published information on Hawaiian Stilts, which quickly colonize newly created wetlands (Pyle 1978, Engilis and Pratt 1993) and forage in ephemeral wetlands (Telfer 1971). Few data exist

on subadult movement patterns for other shorebirds. Robinson and Oring (1996) report on Black-necked Stilt migration, but few banded individuals were seen between the natal and wintering areas. Black-winged Stilts in the western Mediterranean undertake a molt migration (Pienkowski et al. 1976), and Kitagawa (1988) recorded Black-winged Stilts in Japan moving 3 km after fledging, before moving again to wintering sites.

We found no published data for dispersal (i.e. movement from the natal site to a breeding site) in this subspecies or for other stilts. However, if observed movement patterns are indicative of dispersal patterns, we can make predictions regarding population dynamics and population genetics for this species. The extensive movement among wetlands and islands should act to maintain small local populations and stabilize overall population sizes through recolonization after local extinction (e.g. Hansson 1991). Viability modeling for Hawaiian Stilts supports this prediction (Reed et al. 1998). Hawaiian Stilts are suspected to have colonized from the North American mainland (Coleman 1981), but there are no records of the North American race on Hawaii (Banko 1988). If observed movement patterns reflect dispersal patterns, we anticipate a lack of genetic differentiation among islands (see Allendorf 1986). This hypothesis currently is being tested and has important conservation implications. If confirmed, it would mean that localized inbreeding depression as well as local adaptations are unlikely, which means that birds taken for translocation or for captive breeding could be mixed among islands.

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