GROWTH PATTERNS OF HAWAIIAN STILT CHICKS

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ABSTRACT.—We studied chick growth and plumage patterns in the endangered Hawaiian Stilt (*Himantopus mexicanus knudseni*). Body mass of captive chicks closely fit a Gompertz growth curve, revealing a growth coefficient (K) of 0.065 day^{-1} and point of inflection (T) of 17 days. When chicks fledged about 28 days after hatching, they weighed only 60% of adult body mass; at 42 d, birds still were only 75% of adult mass; culmen, tarsus, and wing chord at fledging also were less than adult size. This trend of continued growth to adult size after fledging is typical for most shorebirds. After hatching, captive chicks grew more rapidly than wild chicks, probably because of an unlimited food supply. We found no evidence for adverse effects of weather on the growth of wild chicks. As with other shorebirds, the tarsus started relatively long, with culmen and then wing chord growing more rapidly in later development. Tarsal and wing chord growth were sigmoidal, whereas culmen growth was linear. We describe plumage characteristics of weekly age classes of chicks to help researchers age birds in the wild. *Received 28 Dec. 1998, accepted 20 April 1999.*

Avian growth patterns have been studied primarily because of their relationships to the ecology and evolutionary history of different species (Ricklefs 1968, 1973, 1983; O'Connor 1984; Anthony et al. 1991), and to maximize food yields of domestic animals (e.g., Anthony et al. 1991). Although there is selection for rapid independence of chicks, which should reduce variance in growth rates, intraspecific growth patterns can be variable and flexible because of environmental variability and competing selective pressures (Cooch et al. 1991, Emlen et al. 1991). In studies of wild birds, altricial species have been studied more often than precocial species, at least in part because the former remain in the nest from hatching until fledging.

In this paper we present information on chick growth patterns of the Hawaiian Stilt

(*Himantopus mexicanus knudseni*), a precocial bird that is an endangered subspecies of the Black-necked Stilt. Like all shorebirds, stilts are precocial and nidifugous. Hawaiian Stilts are significantly larger than the nominate race (Coleman 1981) and differ somewhat in adult plumage characteristics (Wilson and Evans 1893, Coleman 1981). Stilts are found on all five major islands in Hawaii, breed exclusively in shallow, lowland wetlands (USFWS 1985), and statewide population counts indicate a steady increase in population size (Reed and Oring 1993). Our specific objectives were to (1) describe patterns of Hawaiian Stilt chick growth from captive and wild birds and compare them to other shorebirds, and (2) provide a method for aging chicks in the field. The last objective was designed for studying pre-adult mortality patterns by providing aging criteria that do not requiring capturing the bird.

METHODS

Captive birds.—Growth data for captive birds came from 15 individuals raised from eggs in 1980 in the Honolulu Zoo. Because chicks were kept in a common enclosure, some competition for food might have occurred, although food was provided *ad libitum*. Because all birds were subject to the same feeding and environmental conditions, inter-individual variability in growth should be minimized. All birds were weighed daily for 42 days to the nearest 0.1 g. Hawaiian Stilts fledge approximately 28 d after hatching (Coleman 1981).

One of the 15 birds was used only for the first 13 d because a bill deformity developed at this time, caus-

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ing the individual to lose mass quickly. A sixteenth bird was not included in the analysis because of aberrant fluctuations in growth. Its mass at hatch was over 5 standard deviations above the mean, and it gained mass rapidly for 11 days. Between days 12–17, however, it lost 25% of its body mass, dropping well below the mean (ca 2 standard deviations); on day 18 it began to grow rapidly again, reaching mean mass for the group 24 d later.

Other variables (culmen, tarsus, and wing chord) were measured less regularly. Measurements were made every 2–4 d after hatching and became less frequent (every 4–10 d) after fledging. Some individuals were measured more often than others. Despite this variation, we were able to derive useful growth patterns for these body measurements. Mass was measured by one person and lengths by another.

A growth curve for body mass was fit to a Gompertz equation ($r^2 = 0.99$; SPSS, Inc. 1995, NONLIN procedure) because it is used most often for shorebirds (e.g., Beintema and Visser 1989a) and we wanted to allow interspecific comparisons to be made (O'Connor 1984). The fit was made on average values for each day from 12–15 individuals. The Gompertz equation has the form

$$W = A \times e^{-e^{-Kt}}$$

where W is body mass (g), A is asymptotic (adult) mass (g), K is the growth coefficient (day^{-1}), t is age (d), and e is the base for natural logarithms. Adult mass came from 43 adult males and 42 adult females (Coleman 1981). Although adult females weigh slightly more than males (mean difference = 7.0 g), the difference is a small percentage (<4%) of total body mass, consequently A was averaged across sexes (202.5 g).

Wild birds.—Wild chicks were captured by hand on the islands of Oahu, Maui, and Kauai in 1978–1980 and 1993. During 1978–1980, we captured chicks with known hatching dates 142 times. Because chicks from the same clutch were not considered to be independent, they were averaged within each clutch (maximum of four chicks averaged per clutch). This resulted in 33 measurements of chicks less than 24 h old (designated day 0; $n = 64$ chicks). Chicks were remeasured every time they were encountered and captured. This resulted in 43 measurements of birds from 2–32 d old ($n = 78$ chicks). We measured mass to the nearest 1.0 g, culmen and tarsus lengths to the nearest 0.1 mm, and wing chord to the nearest 1.0 mm. In 1993, we took measurements on 55 birds ranging in age from hatching to fledging using the above methods. During 1993 we rarely knew the exact age of each chick, so these measurements were used only to determine the relationships among body measurements. Tarsus and wing chord measurements were made on the right side of the chick and the same person made all measurements in 1993. We also noted the presence or absence of an egg tooth. Field measurements from 1978–1980 were made by one person, and in 1993 by another, so values were not compared.

Plumage.—We considered only those plumage characteristics that were visible in the field: fuzzy appearance associated with down, brown versus black cast, presence of an eye ring, etc. We used the above characteristics to describe plumage of weekly age classes. In several cases, plumage descriptions for weekly age classes were incomplete (e.g., lacking description of wing coloration for week 3). Because plumage is essentially the same for chicks of both Hawaiian and Black-necked stilts (Coleman 1981), we supplemented our descriptions of Hawaiian Stilts with plumage observations of wild, known-aged Black-necked Stilt chicks at Honey Lake, California in 1997. Plumage of adult Hawaiian Stilts is different from fledglings (Robinson et al., in press).

Analyses.—Statistical analyses were conducted using version 7.0 of SPSS (SPSS, Inc. 1995). One assumption in comparing body measurements between captive and wild birds is that initial body sizes are equal. To test this, we used multiple analysis of variance (MANOVA) to compare mass and culmen length, tarsus and wing chord measurements between known-aged captive and wild hatch day (day 0) birds. For ages after day 0, we determined whether or not mean values for wild birds fell within 95% confidence intervals for mean values of captive birds. All statistical tests were two-tailed. Values presented are means ± SD.

RESULTS

Growth in captivity.—Growth parameters for the Gompertz equation indicated a growth coefficient (K) of 0.065 and time to inflection point (T) of 17 days. Although chick mass varied little among the 11 individuals on day of hatch (15.7 ± 0.6 g), variability in mass among individuals increased greatly over the first two weeks (60.4 ± 9.2 g), and remained high up to fledging at day 28 (122.5 ± 10.6 g). In general, differences among chick mass at day 14 are consistent until fledging, indicating that chicks that gain relatively more mass in the first two weeks after hatching tend to fledge at a heavier mass than chicks that gain less mass their first two weeks. Captive individuals did not experience a significant mass loss between day 0 (hatch day) and day 1 (paired *t*-test: $t = -0.432$, df = 10, $P > 0.05$).

At fledging, chicks had not attained adult body mass or body measurements. Mass at fledging was 60% of adult mass, culmen length was 67% of adult length, tarsus length was at 66%, and wing chord length was at 55% (adult measurements from Coleman 1981).
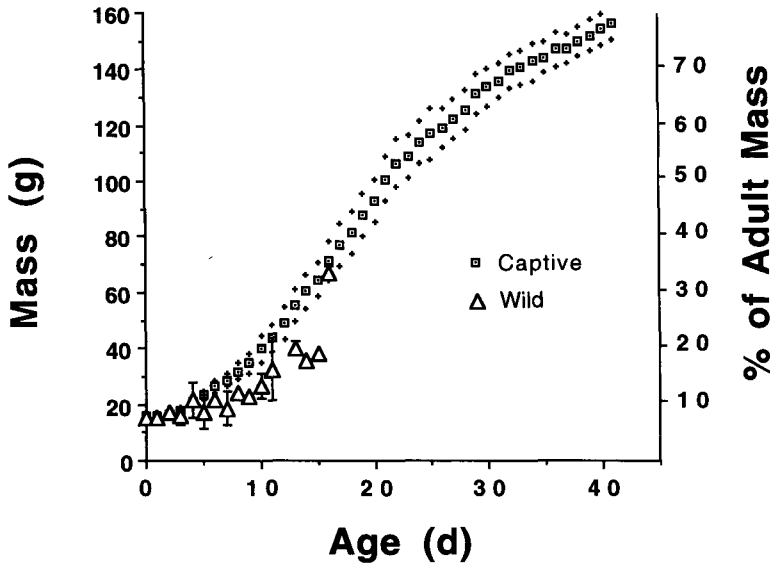
Growth in the wild.—There was no differ-

FIG. 1.   Captive and wild Hawaiian Stilt chick mass and percentage of adult body mass (202.5 g) as a function of age. Values are means ± SE.

ence between mean mass of captive ($\bar{x}$ = 15.7 ± 0.6 g) and wild ($\bar{x}$ = 15.6 ± 1.1 g) chicks at hatch (t = 0.551, df = 40, P > 0.05). The apparent decrease in mass between day 0 (hatch day) and day 1 for wild chicks was not significant (paired t-test: t = 0.585, df = 12, P > 0.05). From days 1 to 17, masses of same-aged wild birds typically fell within the 95% confidence interval of captive birds, though below the mean. In three comparisons (day 9, 14, 15), the mass of wild birds fell below the 95% confidence interval for captive mass. Mass gain with age generally followed a sigmoidal pattern, with individuals not reaching an asymptote until after 42 days of age (Fig. 1). Similarly, from days 1 to 17, mean wing chord of same-aged wild birds fell within the 95% confidence interval of captive birds, with the exception of days 9, 14 and 15, when mean wing chord measurements for wild birds fell below the 95% confidence interval. Growth of the wing chord also followed a sigmoidal pattern, although the slope of the curve was less steep for wing chord growth than it was for mass gain (Fig. 2). Mean culmen length and mean tarsus length did not differ between wild and captive birds from days 1 to 17. Mean culmen growth for both wild and captive chicks was relatively linear with increasing age (Fig. 2).

Relative growth rates.—Relative growth rates among different parts of the body can be assessed without reference to age. We found tarsus length to be long in early development relative to culmen and wing chord, and it continued to grow at a faster rate than the culmen throughout development. Culmen and wing chord grew at approximately the same rate in early development until wing chord reached about 40 mm; as wing chord continued to grow, culmen length growth rate slowed considerably. Changes in wing chord and body mass were similar throughout the growth period observed (Fig. 3). Changes in tarsus length and body mass also were similar until individuals reached approximately 80 g, when tarsus growth slowed.

Plumage.—Using field data from known-aged chicks, we constructed a table of weekly plumage characteristics for Hawaiian Stilt chicks (Table 1). The presence or loss of down, as well as overall body color, appear to be the two best indicators of chick age in the wild for weeks 1–3. Aging during this time is more precise if one can determine the presence and condition of primary sheaths; this cannot be done, however, without chicks in hand. Specifically, in week 1 chicks are entirely covered with down, and primary sheaths are absent. The dorsal surface of the body in-
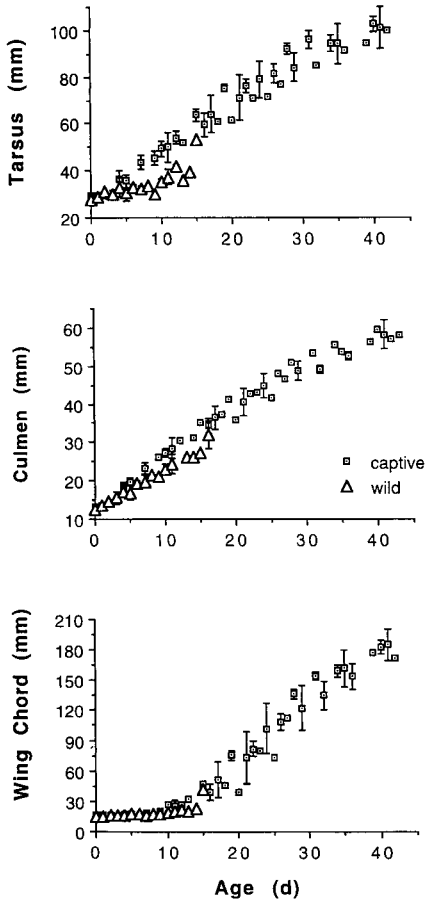
FIG. 2. Growth patterns for wing chord, culmen length, and tarsus length of captive and wild Hawaiian Stilt chicks.

FIG. 3. Relative growth rates of three body measurements of wild Hawaiian Stilt chicks compared to body mass.

cluding head, neck, back, and wing is mottled black, golden brown, and white; the ventral surface is creamy white. In week 2, the head begins to turn brown and is distinctly lighter than the rest of the body. Mottling on the neck changes to a more solid pattern of gray and tan. Most importantly, primary sheaths emerge on day 12. During week 3, down begins to disappear, giving chicks a sleeker appearance. Overall body coloration changes from mottled black, golden brown, and white to plain gray and white, and primary sheaths are broken about day 16. In all cases where we had information on both subspecies, plumage descriptions of known-aged Black-necked Stilt chicks matched exactly the plumage descriptions of known-aged Hawaiian Stilt chicks up to and including six weeks of age.
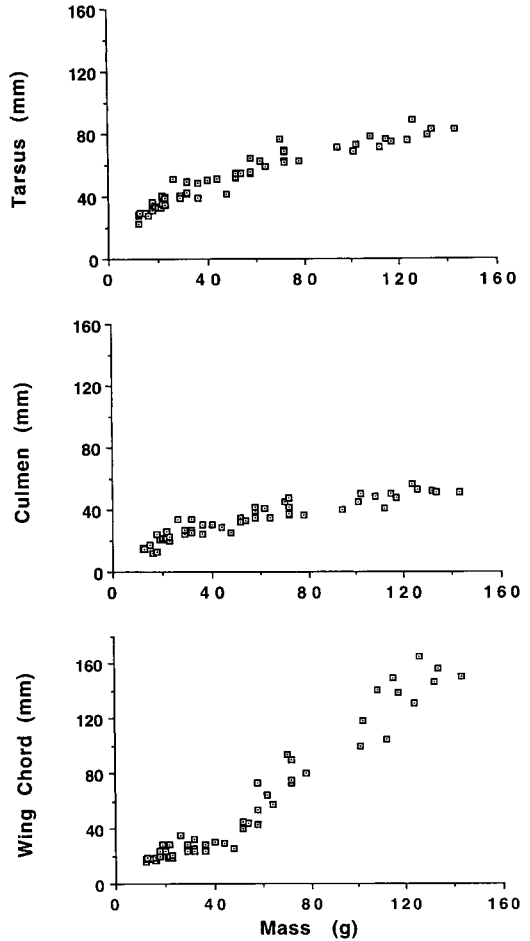
From 4–6 weeks, age classes can be differentiated by the presence of tail feathers, the ability to fly, and the presence of an eye patch and eye ring. In week 4, tail feathers emerge and the eye patch and eye ring become visible. During week 5, all down is lost, wing feathers are fully developed enabling short distance flight (up to 1.5 m), and the eye patch is distinct. Finally in week 6, chicks are capable of prolonged flight.

As with other shorebirds (Clark 1961), the egg tooth typically was lost after the first day and always was gone after 48 h.

DISCUSSION

Because shorebird chicks feed themselves, they hatch with well developed legs and a

TABLE 1. Plumage characteristics of wild Hawaiian Stilt chicks according to weekly age classes.

	Down	Overall body color	Head	Neck	Back
Week 1	Covers entire body	Dorsal mottled black, golden brown & white; Ventral white	Dorsal mottled black, golden brown & white; Ventral creamy white	Dorsal mottled black, golden brown & white; Ventral creamy white	Contours ~day 5; mottled black, golden brown & white
Week 2	Covers entire body	Dorsal mottled black, golden brown & white; Ventral gray to creamy white	Beginning to turn brown; lighter than rest of body	Dorsal gray & tan; Ventral creamy white	Mottled black, golden brown & white
Week 3	Beginning to lose; Some on head, lower neck & upper back; tail downy	Gray & white from distance	Dorsal brown; Ventral creamy white	Dorsal gray; Ventral creamy white	Mottled black & golden brown
Week 4	Some remaining on head, at base of secondaries & at tips of tail feathers	Black & white from distance	Black on top; otherwise brown	Dorsal gray; Ventral creamy white	Mottled black & golden brown
Week 5	None	Black & white	Mostly black w/brown flecks	Dorsal gray; Ventral white	Mottled black & golden brown
Week 6	None	Black & white	Mostly black w/brown flecks	Dorsal gray; Ventral white	Mottled black & golden brown

TABLE 1. EXTENDED

	Wing	Tail	Primary sheaths	Secondaries	Humeral tract	Eye patch	Eye ring
Week 1	Mottled black & golden brown w/white perimeter	Black w/golden brown tips	Not present	Not present	Not present	Not present	Not present
Week 2	Mottled black & golden brown w/white perimeter	Black w/golden brown tips	Present ~day 12	Slightly brown	Brown	Not present	Not present
Week 3	Mottled black & golden brown w/gray leading edge	Black w/golden brown tips	Broken ~day 16	Mottled black & brown	Brown	Not present	Not present
Week 4	Mottled black & golden brown w/gray leading edge	Feathers present for first time	In broken sheaths	Brown	Brown	Just visible; white	Present & black ~day 25
Week 5	Fully developed; can fly short distances (5′); black w/brown tips	Fully feathered; Black w/golden brown tips	In broken sheaths; Free & molt complete ~day 33	Brown	Brown	Distinct; white	Present; black
Week 6	Flying	Black w/golden brown tips	Not present	Brown	Brown	Distinct; white	Present; black

partly developed bill; wing development begins later and is rapid once started (Galbraith 1988, Thompson et al. 1990). Growth patterns are variable among species (Holland and Yalden 1991; Starck and Ricklefs 1998a, b). For example, body mass at fledging as a percentage of asymptotic adult body mass varies in shorebirds (Scolopacidae and Charadriidae) from 53% to 91% (Beintema and Visser 1989a). In addition, it has been suggested that shorebirds have a higher growth coefficient (K) than other terrestrial, precocial birds (Beintema and Visser 1989b). Of 15 species reviewed by Beintema and Visser (1989a), K ranged from 0.051 to 0.158, and the inflection point (T) ranged from 5.5 to 23.8 d after hatch. Not surprisingly, body size is positively correlated with the inflection point and negatively correlated with the growth coefficient. That is, larger species reach the half-way point in growth at a relatively larger size, and grow at a slower rate in proportion to their adult body size, than do smaller species. Hawaiian Stilts conform to these patterns.

Shape of growth curves.—Captive Hawaiian Stilt chicks grew from approximately 15 g at hatching to 125 g at fledging, attaining only 60% of adult body mass when they fledged. Culmen, tarsus, and wing chord also were still growing at fledging, well below adult sizes, and did not reach adult values until after 42 days after hatching. Culmen and tarsus sizes increased rapidly between hatching and fledging, with culmen growth generally following a linear trajectory and tarsus following a slightly sigmoidal pattern. Wing chord growth was sigmoidal, with slow growth from hatch day to day 12 followed by a substantial increase in growth rate when chicks reached 13–15 days old.

Mass loss in the first 24–48 h after hatch has been reported in some shorebird species (e.g., Lapwing, *Vanellus vanellus*; Galbraith 1988) and is attributed to movement away from the nest cup soon after hatching. Although Hawaiian Stilts also leave their nest cup within a day of hatching, we found no significant mass loss for captive or wild chicks from day of hatch to day 1. Differences in the distance traveled and the amount of food available in the first 24 h may explain interspecific and intraspecific differences in shorebird mass loss immediately after hatching.

Reasons for variation in shorebird post-hatching mass loss require further investigation.

Comparison of captive and wild chick growth.—Captive and wild chick masses did not differ significantly for most ages; when they differed, wild birds were lighter than captive birds. By the end of week 1 captive chicks generally were growing at a faster rate than wild chicks for all growth parameters measured. This trend mirrors results from other studies of precocial birds (Beintema and Visser 1989a). In most cases, captive and wild chicks have similar growth curves, with more variation in the growth of wild chicks (Visser and Ricklefs 1993). Faster growth in captivity could be due to an unlimited food supply, while slower growth in the wild could be attributed to colder weather, which increases the costs of thermoregulation and reduces the amount of time that chicks can spend foraging. A study of time budgets in the field of three precocial charadriiform species revealed that during adverse weather, young chicks were brooded for 75% of the daytime, and as a result, they could not obtain enough food to satisfy their energy requirements (Beintema and Visser 1989a). In contrast, during good weather conditions, chicks foraged almost continuously once they were able to thermoregulate.

Beintema and Visser (1989a, b) hypothesized that for shorebird species, cold temperatures and cold with rain are the main causes of slower chick growth in the wild. Specifically, temperatures dropping below 15° C slowed chick growth. In Hawaii, temperatures in coastal wetlands where Hawaiian Stilts breed rarely fall below 21° C, and there are no records of temperatures as low as 15° C. In addition, rains at coastal areas typically are short-lived. The fact that growth was slower in wild chicks despite temperatures above 15° C suggests that temperature itself is not the main factor affecting slower Hawaiian Stilt chick growth in the field. At warmer temperatures, Pierce (1986) observed faster growth in other stilt species. Either a different threshold applies to Hawaiian Stilts or differences were due to food availability (Beintema 1994).

Comparison to other species.—Hawaiian Stilts grow slowly in comparison to other shorebirds. Of the 42 growth coefficients

Starck and Ricklefs (1998a) reported for 27 species of shorebird, only 5 were lower than what we calculated for Hawaiian Stilts, and all came from heavier species. The only published estimates of *Himantopus* growth coefficients are Starck's and Ricklefs' (1998a) calculations from Pierce's (1986) data on Pied (*Himantopus himantopus leucocephalus*) and Black (*H. novaezealandiae*) stilts. These species have lower adult masses (129 g and 130 g, respectively) than do Hawaiian Stilts, but do not fledge until a later age. Hawaiian Stilts fledge approximately 28 days after hatching; Pied Stilt chicks do not fledge until they are 34 d, and the Black Stilt fledges even later (at 46 d; Pierce 1986). Similar to the Hawaiian Stilt, both species continue to grow after fledging. However, based on data presented by Pierce (1986: fig. 6), Pied and Black stilts fledge at a higher percent of their adult body mass. Consequently, despite the longer time to fledging, Pied and Black stilt growth coefficients are consistent with expectations based on their adult size ($K = 0.175$ and 0.129 respectively; Starck and Ricklefs 1998a). A K of 0.074 would be expected for the 202.5 g Hawaiian Stilt (Beintema and Visser 1989a), but we observed $K = 0.065$ for Hawaiian Stilts in captivity (and possibly lower in the field; Fig. 1). Starck and Ricklefs (1998a) also reported faster growth coefficients for the European Avocet (*Recurvirostra avosetta*; $K = 0.213$ and 0.171 from two different studies), which is similar in mass to Hawaiian stilts (168 g and 250 g, respectively). Although the relationship between body mass and K in Charadriiformes, is poor ($r^2 = 8\%$, $n = 75$ species; Starck and Ricklefs 1998b), these data demonstrate that the slow growth rate observed in Hawaiian Stilts is not a characteristic of the Recurvirostridae.

We do not know why Hawaiian Stilts have slow growth. The two obvious hypotheses do not provide satisfactory explanations. First, growth rate could be correlated with latitude. Tropical environments provide a longer breeding season, and growth rates of tropical altricial species are lower than are those of taxonomically related temperate species (Ricklefs 1976, Oniki and Ricklefs 1981). The Hawaiian Stilt breeding season lasts six months (Coleman 1981). Despite this, neither the incubation nor fledging period is prolonged.

Worldwide, stilts average 22–26 days of incubation (Johnsgard 1981), which incorporates the Hawaiian Stilt's incubation length of 25 days (Colemen 1981). As noted above, the fledging time is shorter in this species than in others of its genus (Johnsgard 1981, Pierce 1986) so there is no extended time as a chick. There are no studies of which we are aware comparing growth rates of precocial species across a latitudinal gradient, but it would be an interesting assessment.

Second, the lower growth rate could be a consequence of evolving in an island environment where predation rates might have been relatively low before human occupancy, and selection for rapid growth might have been relaxed. Most recorded mortality of adult Hawaiian Stilts is attributed to introduced species (Woodside 1979). However, one would expect slower growth to be associated with an older age at fledging, which does not occur. In contrast, the Hawaiian Stilt fledges at a smaller percent of adult body mass than do other stilts, resulting in an extended post-fledging growth period.

Estimating age.—Ideally, estimates of chick age would be based on a trait that changes rapidly and monotonically throughout growth. One problem with this method is that often no one trait is ideal throughout the entire growth period. Rather, traits differ in their accuracy for aging as chicks become older. For example, measurements of tarsus and wing chord for Hawaiian Stilts are not useful for aging chicks at early and late ages because of their sigmoidal growth patterns. Using mass as an indicator of chick age is problematic because it fluctuates rapidly, depending on environmental conditions and when chicks are weighed in relation to their last feeding. For Hawaiian Stilts, culmen length may be the most useful parameter for aging chicks because its growth trajectory is fairly linear. Because it typically has a constant growth rate throughout the chick stage, culmen length has been used to age chicks of other shorebird species in the wild (Beintema and Visser 1989a). However, even for traits that tend to vary linearly and monotonically throughout development, there is a tremendous amount of individual variation in daily growth. Unfortunately, this individual variation is magnified by measurement error when all measurements

are not made by the same person. Thus, determination of chick age using body measurements and mass, regardless of the species, should be viewed as approximate at best.

As a result, we decided to describe general plumage patterns for Hawaiian Stilt chicks of known age in the field to set up criteria for establishing weekly age classes for chicks, defined by the presence or absence of specific plumage characteristics. The ability to identify approximate chick age in the field without capturing young of this endangered species could aid in management by helping to identify the age at which chicks disappear. To this end, we found definitive differences between plumage characteristics of specific age classes of Hawaiian Stilts. This should increase abilities to assess survival, the least understood life-history component of this species (Reed et al. 1998).

We found plumage characteristics to be useful for identifying weekly age classes of Hawaiian Stilts. Because culmen length is similar for captive and wild chicks and has a linear positive relationship with age throughout development, a combination of culmen length and plumage description may be the most accurate way to age wild Hawaiian Stilt chicks. Relying primarily on plumage characteristics, specifically because they are non-invasive, and supplementing these observations with culmen lengths if chicks are captured, will help minimize interference in this endangered species while providing managers with a tool for monitoring reproductive success and population numbers. Because adults and fledglings differ in plumage patterns, it also will allow accurate monitoring of reproductive success before molt.

ACKNOWLEDGMENTS

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