THE CONDOR

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

Volume 86 Number 2 May 1984

The Condor 86:105–117

BIOLOGY AND CONSERVATION OF THE LAYSAN DUCK (*ANAS LAYSANENSIS*)

DANIEL W. MOULTON

AND

MILTON W. WELLER

ABSTRACT.—A two-summer, mark-recapture study of Laysan Ducks (*Anas laysanensis*) resulted in a population estimate of 510 birds with over 90% of the birds marked. Individuals seemed long-lived with the low reproductive rate common to K-selected species.

Nesting occurred in spring and early summer in spite of the subtropical climatic regime. Nests were mainly in clumps of grass (*Eragrostis*) and hatching success was low. Duckling mortality due to exposure was common during rainstorms, but no direct predation was noted. Pair-bond behavior resembled that of continental populations of Mallards (*Anas platyrhynchos*) but males tended to return to mates after brood-rearing or loss of brood or nest. Year-to-year mate switching occurred more than half the time, even when previous mates were alive. Males did not assist in care of the brood.

During spring and summer, ducks of all ages fed heavily on invertebrates. Adult brine flies (*Neoscatella sexnotata*) on mud flats around the lake were the major food of ducks of all ages. Radio-marked pairs consistently used the same upland areas during the day. At night, most ducks moved to a lake on the island to feed, and to drink in communal areas at freshwater seeps. Feeding and drinking was dominantly crepuscular and nocturnal at the lake, but laying hens or hens with broods sometimes fed throughout the day as well.

Conservation of the species requires monitoring of duck populations and habitat conditions, and surveillance for accidentally introduced predators such as rats. The lake is vital to the success of the species, and it is unlikely that a significant population could survive on terrestrial resources alone. Intensive management will be necessary only if blowing sands fill the lake, predators become established, or the vegetation is seriously damaged in some way.

The Laysan Duck (*Anas laysanensis*) is one of several island endemics derived from the far-ranging Holarctic Mallard (*Anas platyrhynchos*). Restricted to one tiny island of the Hawaiian leeward islands (Fig. 1), the Laysan Duck has been near extinction due to human activities and, after many years of protection, still remains on the Endangered Species List. Another Mallard-like island endemic, the Mariana Mallard (*A. platyrhynchos oustaleti*) may number fewer than six individuals; the Hawaiian Duck or Koloa (*A. wyvilliana*) occurs mainly on the island of Kauai, but has been successfully reintroduced on Oahu and Hawaii.

Specific objectives of our study were to: 1) determine population size and age structure; 2) evaluate previous census data and devise more reliable techniques; 3) assess the relative importance of various island habitat types to the species; 4) determine annual reproductive rate; 5) describe feeding ecology and foods, where possible, without collection; 6) assess mortality on eggs, young, and adults; 7) assess unique biological features of an insular isolate; and 8) establish management guidelines for preservation of the species.

HISTORY AND STATUS OF THE SPECIES

DISCOVERY AND TAXONOMIC STATUS

Laysan Island was apparently first visited and named by westerners sometime between 1821 and 1826 (Ely and Clapp 1973:19–20). The

Color-banded pair of Laysan Ducks drinking at a fresh water seep along the lake.

Russian ship *Moller* visited Laysan Island on 24 March 1828, and the ship's surgeon, C. Isenbeck, made the first written records of the biota, which later were published by F. H. von Kittlitz (1834). Type specimens of the Laysan Duck were collected in June 1891 by H. C. Palmer and G. C. Munro during an expedition sponsored by W. Rothschild of the Tring Museum, who subsequently described the species (Rothschild 1892). Isenbeck also reported small flocks of Laysan Ducks on Lisianski Island, 225 km west-northwest of Laysan Island (von Kittlitz 1834), but the next recorded visit by Palmer and Munro in 1891 reported no ducks (Rothschild 1893–1900). Clapp and Wirtz (1975) have suggested that the ducks seen on Lisianski Island were never identified and may have been another endemic form. We know of no reliable evidence that Laysan Ducks have ever occurred naturally anywhere except on Laysan Island.

On the basis of the wing speculum, feather patterns, the drakes' slightly upturned central tail feathers, and major breeding displays, the Laysan Duck is clearly a Mallard derivative (Weller 1980:15). It is uncertain whether the Laysan Duck is an independent Mallard isolate or secondarily evolved from the Hawaiian Duck, and this has resulted in varying taxonomic treatment. Recently, it has been recognized as a full species (American Ornithologists' Union 1983).

POPULATION HISTORY AND STATUS

Population "estimates" of Laysan Ducks were summarized partially by Warner (1963:12–14) and in detail by Ely and Clapp (1973:170–171, 175–178) and the U.S. Fish and Wildlife Service (1982). Most estimates have been based upon the numbers of ducks actually seen but included no statistical confidence intervals. Predisturbance population levels are unknown, but the general trends in population numbers during this century are clear. Guano-mining operations on Laysan began in 1891 and continued until about 1904 (Ely and Clapp 1973:23, 27). During this period, duck hunting provided food and sport for members of the mining operation (Warner 1963:11). Fisher (1903:799–800) estimated the population at less than 100 in 1902. Ducks were also killed for food by Japanese plumage hunters who raided Laysan in 1909 and 1910 (Ely and Clapp 1973:40), even though the island had been declared part of the Hawaiian Islands Bird Reservation by presidential executive order of 3 February 1909 (Bryan 1942:187). Even greater impact resulted from the introduction of European rabbits (*Oryctolagus cuniculus*) and by 1911, rabbit numbers had multiplied and seriously damaged Laysan's vegetation (Dill and Bryan 1912: 8). During these years, the Laysan Duck was near extinction. In 1911, Dill and Bryan (1912) estimated a population of from 6 to 12 ducks. In 1912, Bailey (1956) counted seven ducks. When Alexander Wetmore arrived on Laysan in April 1923 to exterminate the rabbits, the island had been almost completely denuded (Wetmore 1925:103). Wetmore counted 20 birds, which may have been the entire remaining population, as no vegetation remained where ducks could hide. As the vegetation recovered, the duck population increased. Brock (1951a) counted 33 ducks including seven young in 1950 and 39 birds in 1951 (Brock 1951b). On the basis of transects, Warner (1963) estimated a population of 688 in 1961. Numerous partial counts were made between 1961 and 1979; the maximum number seen was 287 in 1976 (U.S. Fish and Wildlife Service 1982).

STUDY AREA

Laysan Island, the largest and one of the oldest of the Northwestern Hawaiian islands, is located at 25°46′N, 171°44′W. It is about 225 km east-southeast of Lisianski and 1,463 km west-northwest of Honolulu, Oahu. Laysan Island is the top of a massive submarine volcanic peak that has been eroded far below present sea level and subsequently built up by coralline rock deposited by marine invertebrates and algae. Laysan Island is now part of the Northwestern Hawaiian Islands National Wildlife Refuge. In 1967, Laysan was declared a Research Natural Area by the U.S. Fish and Wildlife Service. To prevent unnecessary human disturbance and accidental introduction of plants or animals, landing permits are granted only for official or scientific activities (Ely and Clapp 1973:3).

Laysan is rectangular (Fig. 1), with the long axis slightly east of north. The Tanager Expedition survey (1923) determined maximum dimensions of 2.9 km (1.8 mi) by just over 1.6 km (1 mi); the total area is about 370 ha (913 acres; Ely and Clapp 1973:3). The center of the island is occupied by a lake which, when full, is about 1.6 km (1 mi) long with a maximum width of about 0.5 km. The actual surface area varies greatly with season and rainfall. In late summer, the lake becomes a series of pools bordered on the west by extensive areas of salt flats (Fig. 1). In 1859, Brooks (1860: 501) reported a maximum lake depth of 9.1 m and a coral bottom. By 1923, Wetmore recorded depths of 0.9–1.5 m with a maximum depth of 4.6 m (Ely and Clapp 1973:18–19). Warner (1963:5) also recorded a maximum

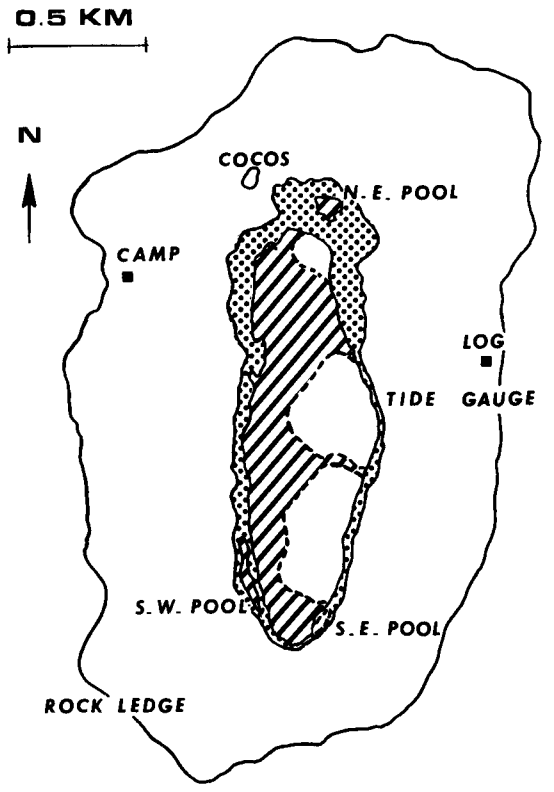

FIGURE 1. Drawing of Laysan Island based on a U.S. Navy photograph of January 1966 showing lake basin (stippled), lake at full pool (slashed); and outlines of pools (white) formed by drying of the lake in late summer, based on a photo taken by Dr. George Balazs on 26 August 1980.

depth of 4.6 m with sand bottom near the eastern lake shore. Because of wind drift of ocean spray and continuous evaporation, the lake water is strongly hypersaline; 12–15% was recorded by Shauinsland (1899:20) in 1896 and Elschner (1915:33) in 1914, and Warner (1963: 5) reported NaCl concentrations of 12–14%. The only invertebrates recorded in the lake are brine shrimp (*Artemia* sp.) and the larval and pupal stages of a dipteran brine fly (*Neoscatella sexnotata*) (Butler and Usinger 1963:27). The lake water and bottom support the growth of red and green algae.

VEGETATION

The vegetation of Laysan is distinctly Hawaiian and highly endemic. The vegetation forms six distinct associations, which grow in roughly concentric rings or belts around the lake (Lamoureux 1963:10–12). A transect from the beach to the beach crest and down the interior slopes to the lake passes through the associations roughly as follows: 1) the *Nama* association is characterized by *Nama sandwicensis,* an herb which forms small, round mounds. This association pioneers on outer beaches and seaward slopes and in places extends over the beach crest to upper parts of the interior slopes. 2) The *Scaevola* association is characterized by the low, dense shrub *Scaevola taccada* and typically occurs just inland of the *Nama* association. Scattered clumps of *Scaevola* occur at various places on lower parts of inner slopes. 3) The bunch-grass association is characterized by *Eragrostis variabilis,* a bunch-grass about 1 m high, which occupies most of Laysan's higher land. On the west side of the island, the bunch-grass association occurs in a wide band whose width exceeds 500 m in some areas. On the east side, the association is less well defined and intergrades with other associations. 4) The *Boerhavia-Ipomoea-Tribulus* association is characterized by low, creeping plants: *Boerhavia diffusa, Ipomoea pes-caprae* (beach morning glory), and *Tribulus cistoides* (puncture vine). The association occurs on lower slopes in a nearly continuous band around the lake. The introduced shrub, *Pluchea indica,* the most abundant shrub on the island, has become well established within the association and forms pure stands of varying size. 5) The *Sesuvium-Heliotropium* association is characterized by seaside heliotrope. *Sesuvium* is a creeping, mat-like plant with succulent leaves that grows only a few centimeters high. 6) *Cyperus laevigatus* is a sedge with a rush-like appearance that grows in pure, dense stands that may reach about 1 m in height. The association forms a band of varying width around the entire lake shore. By 1950, the vegetation had recovered in composition and structure to that described before destruction by rabbits (Brock 1951a). The extent of sandblows and density changes in vegetation since 1951 are unknown; many of the original species either are still present or have been replaced by ecologically similar species.

OTHER NESTING BIRDS

When discovered by westerners, Laysan had 22 species of breeding birds representing six orders (Ely and Clapp 1973:88): 7 albatrosses, petrels, and shearwaters; 5 tropicbirds, boobies, and frigatebirds; 5 terns and noddies; 3 Passeriformes—Laysan Millerbird (*Acrocephalus f. familiaris*), Laysan Honey-eater or Apapane (*Himatione sanguinea freethii*), and Laysan Finch (*Telespyza cantans*); the Laysan Rail (*Porzanula palmeri*); and the Laysan Duck. The Laysan Rail, Laysan Honey-eater, and Laysan Millerbird became extinct around 1923 after rabbits destroyed their habitat. The entire island, with the exception of the outer beaches and salt flats around the lake, is honeycombed with the burrows of shearwaters and petrels.

LOGISTICS AND METHODS

The 1979 field season was from 12 March to 17 August. In 1980, Weller spent 15–17 March on Laysan Island before Moulton's stay from 6 April to 29 August.

Individual ducks or mated pairs were captured with a long-handled net on dark nights using a battery-operated head lamp to locate and to confuse the birds. The following information was recorded for each capture: location and activity; sex and age (Hatch Year = HY, After Hatch Year = AHY); weight, pair and reproductive status if known; and molt and plumage data. Ducklings were classed (aged) by plumage development (Gollop and Marshall 1954): Class I—all down; Class II—more down than contour feathers; Class III—more contour feathers than down. In 1979, the numbers of primary flight feathers were counted on both wings for a large sample of ducks; some wing tracings also were made. All ducks old enough to accept a #5 band were banded with USFWS incoloy bands. In 1979, birds were banded with numbered, colored, plastic bands (National Band and Tag Co.) to facilitate observation of individuals and pairs. In addition, in 1980, numbered, metal web tags were used on ducklings too small for a #5 band. In 1979, population censuses were made throughout the study period. Population estimates were derived from the ratios of marked to unmarked birds observed at the lake at dusk with binoculars and spotting scope.

In 1980, radiotelemetry was used to locate nesting females and record daily activities. DAV-TRON (Minneapolis, MN) transmitters weighing approximately 20 g each were affixed to the ducks with wire harnesses (Dwyer 1972). Radio-tagged pairs were banded with colored plastic bands for individual visual recognition. Radio-tagged ducks were tracked at various times of the day and night for a three-month period.

Because no birds could be collected, observation was the only means of assessing food use. In 1979, 8-mm time-lapse movie footage (1 frame/min) was obtained during daylight hours to measure diurnal activity at feeding and drinking areas along the lake. In 1980, time-lapse footage also was obtained at night by use of a synchronized flash, powered by a 512-volt battery pack. Time-lapse films were analyzed by use of a Time-lapse Data Analyzer Projector with automatic frame counter.

Data were gathered to provide monthly indexes of abundance for adult brine flies and larvae of the moth *Agrotis dislocata*. Adult brine flies were sampled by three 1-m long surface sweeps with an insect net (38 cm diameter opening) at three sampling stations around the lake (north end, tide gauge, and southwest side). Core samples of the lake bottom were taken in both years to confirm the presence of brine fly larvae. Larvae and pupae of *Agrotis* were sampled under vegetation (*Ipomoea, Tribulus, Nama, Boerhavia,* and *Portulaca*) in three areas of the island (north end, east side, and west side) by straining the sand from a circular sample area 38 cm in diameter and 15.2 cm deep. In 1979, some samples of brine shrimp were taken from the lake with an aquatic sweep net. A conductivity meter (Yellow Springs Instrument Co.) was used to measure salinity of water in the lake, ocean, and at seeps in the sand along the lake shore.

RESULTS

POPULATION ESTIMATION

Our work in 1979 indicated that the population of mature Laysan Ducks (AHY) was about 480 birds (Fig. 2). Adding recruitment, a population of about 510 birds entered the winter in 1979–1980. We have no reason to suspect that the 1980 population was different from 1979. During the two years of study, 502 ducks were banded; 452 AHY and 8 young-of-the-year (HY) in 1979, and 29 AHY and 21 HY in 1980. Ten ducks that had been banded before our study were given new incoloy bands although the numbers on their original bands were still legible. Two of the ducks had been banded as HY birds in 1967 and thus were 12 years old (Table 1); moreover, four of eight HY birds banded in 1968 were still alive in 1979.

We found it very difficult to obtain reliable

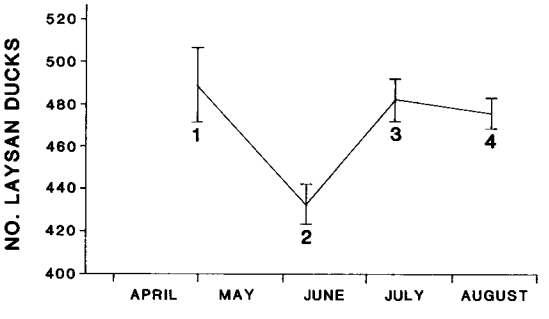

FIGURE 2. Population estimates, with 95% Confidence Intervals, of Laysan Ducks, 1979. #1, estimate = 489 based on 14 censuses (range 432–540 total ducks and 269–296 marked) run between 6/1 and 6/14; #3, estimate = 482 433 based on 8 censuses (range 419–447) (392 ducks marked) run between 6/1 and 6/14; #3, estimate = 2/482 based on 6 censuses (range 469–494) (419–427 ducks marked) run between 7/3 and 7/16; #4, estimate = 476 based on 6 censuses (range 470–488) (447 ducks marked) run between 8/4 and 8/15, 1979.

TABLE 1. Recaptures in 1979 of all known surviving Laysan Ducks banded prior to this study.

Year banded	Total no. banded	Age of banded sample		No. still alive in 1979		Age or minimum age
		AHY[1]	HY[2]	AHY[1]	HY[2]	
1958	58	—	—	0	0	—
1961	204	—	—	0	0	—
1963	17	—	—	0	0	—
1964	117	—	—	0	0	—
1965	25	—	—	0	0	—
1966	38	—	—	0	0	—
1967	27	21	6	0	2	12
1968	24	16	8	2	4	11
1971	7	6	1	1	1	8

[1] After hatch year.
[2] Hatch year.

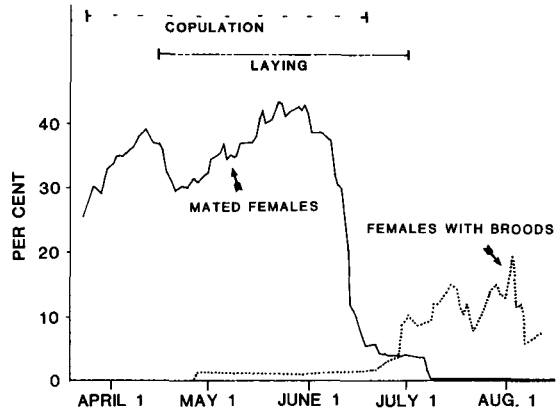

FIGURE 3. Reproductive cycle of the Laysan Duck during 1979. Records of laying and copulation reflect only time period and not incidence. Percentage of females mated or with broods reflects incidence at times of observation, and may not infer that all females are not mated at some time during the reproductive period.

estimates of Laysan Duck populations, especially in the limited time available to landing parties checking on the status of the species. The walking of line transects during the day was not an effective way of censusing because the ducks did not flush readily and were especially difficult to see in their favored resting cover (*Eragrostis*). Some heavily used cover types, e.g., *Pluchea* and *Scaevola,* were virtually impenetrable and could not be censused effectively. Moreover, damage to petrel and shearwater burrows was a serious problem.

We found that the best way to census Laysan Ducks during a few days in summer was to walk around the lake shore on dark nights using a light to observe and count ducks. Counts could also be made during the twilight periods, but more ducks were present at the lake at night. The maximum number of ducks actually observed could be doubled as a rough approximation of the total population. However, this method was less satisfactory during August because ducks seemed to drift away from the lake and into the uplands in late summer, a phenomenon possibly related to a decrease in numbers of brine flies around the lake at that time.

REPRODUCTIVE CHRONOLOGY AND PATTERN

The major reproductive effort resembled that of any northern hemisphere bird in that it was seasonal and occurred in early summer. In March during both 1979 and 1980, we saw no evidence of partly grown ducklings that would have hatched in winter. Moreover, many ducks were paired, and the sequence and phenology of pair bond formation, laying, and brood-rearing was typical of a continental Mallard population.

Analysis of movies of major breeding displays, which took place primarily on the lake at the tide gauge, showed that all displays were very similar to those of the Mallard. The whistle of the grunt-whistle display in Laysan Ducks was inaudible to us. Copulations were observed on the lake, the ocean, and on land.

The general pattern of reproductive behavior noted in 1979 was typical of many species of continental ducks, with a long pair-bond period, and a decline in pair bonds as nesting advanced and broods appeared (Fig. 3). Although pair status is expressed in Figure 3 as a percentage of mated hens on various observation times, this included observations of hens that had already been abandoned by their mates, so a higher total percentage of females was paired during the entire breeding season. Ideally, data on the nesting attempts and date of laying should have been established from nests; however, only a few nests were found each year. Additional data on laying were derived by palpating captured females. The best indication of effective or realized nesting effort was derived from the observation of broods.

The total number of ducklings observed and the mean number per hen differed between years (Fig. 4). This pattern also was reflected in age classes and weights of ducklings observed (Fig. 5). Because of the more inclement weather in the winter of 1980, lake water levels were higher than in 1979 and may have increased production of brine flies, making earlier breeding possible.

PAIR BONDS

Many females were paired in early March of both years. The sex ratio of the trapped sample was 1.25 ♂/1.00 ♀, which resulted in considerable sexual harassment of hens by unmated

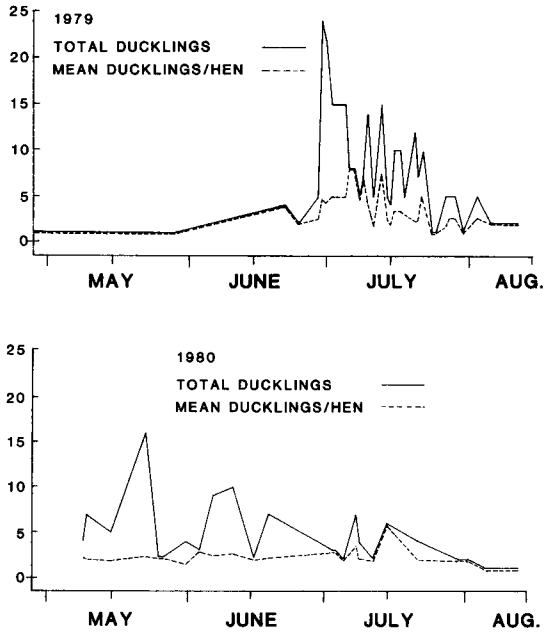

FIGURE 4. Mean number of ducklings per hen and total ducklings observed, 1979 and 1980.

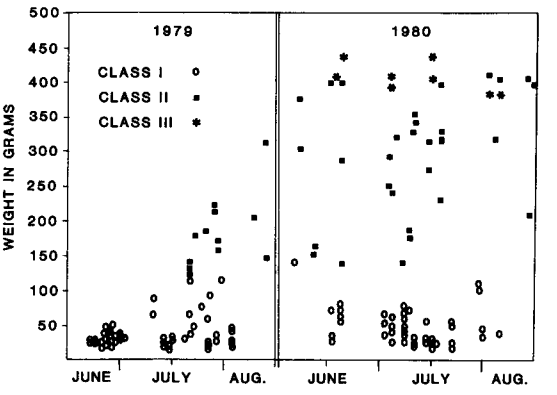

FIGURE 5. Weights of ducklings by age class and time, 1979 and 1980.

males. The pair bond between mated ducks temporarily broke shortly after hens began full-time incubation. Drakes took no part in brood rearing. Based on radio-tagged birds, hens that lost a clutch or brood paired again with the original drake. Pair bonds broke again when the drakes began to molt in mid-summer.

Data recorded in 1980 on known pairs from 1979 suggested that although mate retention was strong, mate switching occurred over half of the time (Table 2). We kept year-to-year records of some members of 33 pairs: 4 hens were known dead, so a maximum of only 29 could have remated. In 10 cases, hens were seen with broods, but mates were unknown. Eight retained the same mates. Hence, 11 (58%) had new mates: 6 hens, 2 drakes, and both sexes of 3 pairs that switched mates.

NESTING

Two nests of three eggs each were found in 1979; one active nest in *Eragrostis* and one abandoned nest in *Heliotropium*, both near the southwest pool. The active nest was abandoned owing to predation of all three eggs by Laysan Finches (Fig. 6). Seven nests were located and studied in 1980 (Fig. 6). Nine hens were radio-tagged during the study. One of these (No. 968) died early in the study, and one (No. 916) was incubating near the camp when tagged. Seven hens were radio-tagged before their nesting status was known. Of those seven, six nested (one apparently did not attempt to nest), suggesting that most mated AHY hens attempted to nest in 1980.

TABLE 2. Pair bond tenacity in 19 pairs of Laysan Ducks marked in 1979 that could have remated in 1980 (i.e., mates were known to be alive).

Status in 1980	No. pairs	Percent
Same mates as in 1979	8	42
Female with new male	6	32
Male with new female	2	10
Both switched mates	3	16
Total	19	100

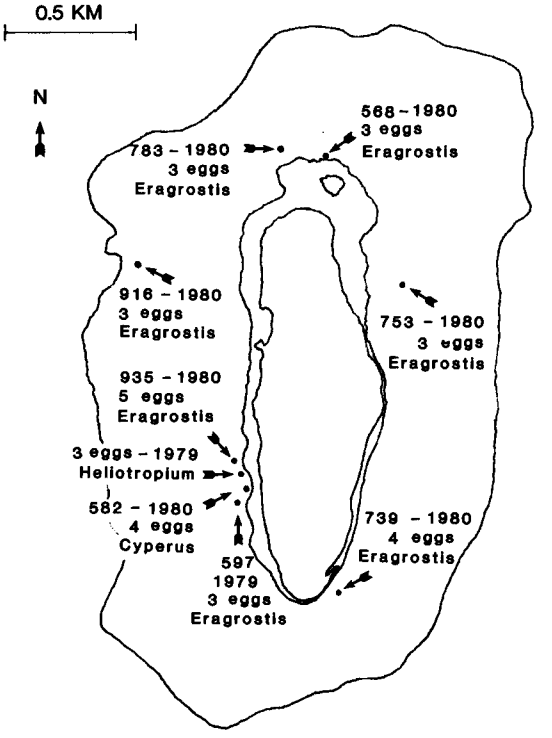

FIGURE 6. Locations, clutch size, and cover type for nests located in 1979 and 1980.

Clutch sizes observed in 1980 were 3, 3, 3, 3, 4, 4, and 5. The largest clutch reported was six eggs (Fisher 1903).

Of the seven active nests studied in 1980, only one hen (No. 753) produced ducklings. Six of the seven nests, including the one that hatched two ducklings, suffered at least some egg predation by Laysan Finches. Several eggs failed to develop. One nest (of female No. 582) was abandoned with four undamaged eggs, but only one of the eggs had embryonic development. Six nests were in *Eragrostis* clumps and one in *Cyperus*. Nests were on the ground deep within the base of vegetation such as *Eragrostis,* and were lined with dead grass and very little down. Nest sites were scattered all over the island (Fig. 6), some being far from the lake. Most broods were first captured or observed near the tide gauge or at the southwest pool because hens led their broods to those areas soon after hatching. The attraction of those two areas seemed to be the availability of drinking water, and conductivity measurements confirmed that these were seepages of fresh water. Finches and Bristle-thighed Curlews (*Numenius tahitiensis*) also drank regularly there.

REPRODUCTIVE SUCCESS

At least 25 different hens had broods for some period of time during the 1979 nesting season, with about 70 ducklings observed (Fig. 4). Many hens lost or abandoned nests before hatching. Brood sizes were small, ranging from one to eight (downy class IA) per hen, but most broods were three to five and declined to two to three as they neared flying age. Because broods of several ages commonly merged, relative figures or mean brood sizes may not be meaningful. Only eight HY ducks were banded with #5 metal bands in 1979 because of the small size of the ducklings. However, using an estimate of 30 ducklings fledged during 1979, less than a 6.25% recruitment rate was experienced during 1979 for an estimated population of 480 ducks. At least 30 hens had broods in 1980, with a total of 73 ducklings observed (Fig. 4). Although survival seemed better in 1980 than 1979, no data are available except from trapping. In 1980, 21 Class III birds were banded, suggesting some annual differences in production.

BODY WEIGHT PATTERNS

Birds captured throughout the season were weighed and reweighed to determine general patterns of weight relative to reproductive stage. The typical pattern in continental Mallards is that males outweigh females at all stages, and during the fall, young males outweigh adult females. This was not the pattern in Laysan Ducks, as evidenced by weight data gathered in 1979 (Table 3). During March, April, and May, mean weights of females, whether mated or unmated, generally exceeded those of males. Presumably, oviduct and ovary size account for this, and males were perhaps at less-than-peak weight because of courtship activities. During June–August, the pattern was reversed, with males generally heavier than females except for a few laying hens. Unmated birds tended to be lighter than mated birds. Females with broods were the lightest of all mature birds, suggesting that incubating hens could not maintain normal weight on their shortened foraging schedules.

During 1979, weights of the oldest ducklings (Fig. 5) in early August were less than half those of mature birds. Thus, considerable growth must have occurred before winter, when food may have been scarce and the weather more severe.

MOLT

Like other anatids, Laysan Ducks underwent a simultaneous wing molt and were flightless at that time. The molt pattern was the same in both sexes, but the sequence occurred slightly earlier in males than females. Males in wing molt first were observed on 14 July 1979, whereas the first females were noted on 22 July. Both were well feathered by mid-August, suggesting that wing molt took three to four weeks—a pattern typical of mainland ducks.

MORTALITY

The Laysan Duck fits the general observation that vocalizations of island ducks are less conspicuous than those of continental species (Weller 1980). For example, although there are no mammalian predators on Laysan Island, these ducks seem to lack the noisy "persistent quacking" call of continental Mallards that some workers consider is used for the declaration of territory (Abraham 1974) but that may also help females to assess the presence of predators in a potential nesting area.

Although five or more observers were present on Laysan during most of the breeding seasons of 1979 and 1980, no duckling mortality due to predation by Great Frigatebirds (*Fregata minor*) or other large seabirds was noted. However, nine ducklings died during a rainstorm of 1.45 in. of rain during the night of 19–20 July 1979. Ducklings often became separated from the hens, possibly owing to the distances they traveled while feeding. Such ducklings were highly susceptible to exposure during bad weather.

Survivorship of Laysan Ducks is high once

TABLE 3. Mean weight (SD) (sample size) of Laysan Ducks by time periods for 1979. This includes reweighing of the same individuals when recaptured.

	March 3–April 8	April 9–May 8	May 9–June 7	June 8–July 7	July 8–August 6	August 7–21
♂ mated	477.7 (21.6) (15)	460.3 (25.9) (45)	443.9 (26.6) (39)	445.7 (32.7) (24)	471.1 (31.7) (17)	419.3 (23.4) (7)
♂ unmated	453.9 (32.7) (14)	450.0 (44.8) (72)	442.8 (39.0) (75)	441.6 (44.1) (51)	451.7 (57.4) (71)	412.3 (37.5) (18)
♀ mated	516.2 (54.5) (13)	464.2 (43.5) (44)	469.6 (45.1) (35)	438.1 (40.0) (15)	439.7 (34.3) (22)	408.0 (46.3) (7)
♀ unmated	488.0 (94.0) (8)	466.4 (49.4) (47)	453.3 (50.4) (42)	434.2 (45.1) (29)	433.3 (45.8) (47)	402.6 (34.9) (8)
♀ laying (only)	555.9 (70.5) (3)	480.1 (39.9) (20)	469.3 (49.0) (12)	433.0 (85.0) (6)	404.8 (34.7) (9)	456.0 (65.1) (2)
♀ with brood	538.0 (—) (1)	506.0 (60.9) (10)	473.9 (64.0) (12)	430.7 (66.1) (12)	397.2 (36.5) (26)	413.7 (28.9) (3)

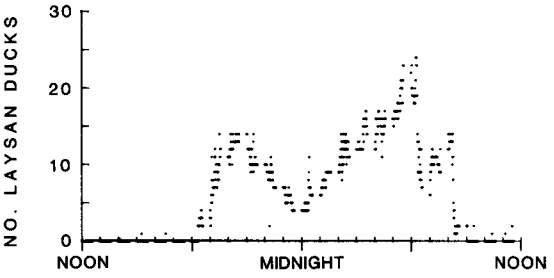

FIGURE 7. Use by Laysan Ducks of freshwater seeps by the lake shoreline, based on counts in time-lapse photos taken at a rate of 1/min, in 1980.

they reach maturity. Adults died from collisions with large seabirds and starvation; in addition, several females apparently were sexually attacked by males in 1980, and at least one of them died as a result. In 1980, 10 AHY ducks banded in 1979 were found dead. This must have represented a significant portion of all mortality from August 1979 to August 1980. This low mortality seemed in balance with low recruitment.

DIEL ACTIVITY PATTERN

Analysis of time-lapse movie films from 1979 and 1980 supported the general observation that ducks were inactive during the brighter and warmer portion of the day. At twilight, both early and late, ducks were common at communal drinking and feeding areas at the tide gauge and southwest pool. Most birds also were actively feeding much of the night. Nocturnal footage during 1980 revealed extensive drinking and feeding along the lake shorelines much of the night (Figs. 7 and 8). Whereas nocturnal feeding is not uncommon in other ducks (Klima 1966, Swanson et al. 1976), the lack of daytime activity in the same area is unique.

HABITAT USE AND TERRITORIALITY

During 1979, several hundred repeat sightings were recorded for each sex and were plotted

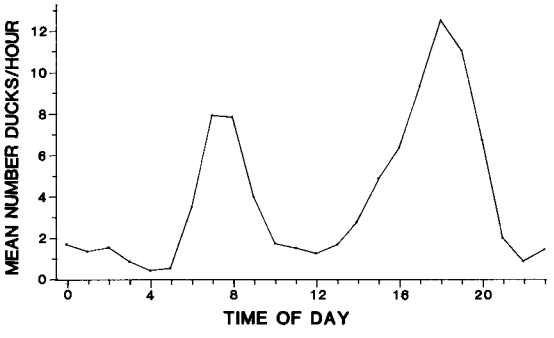

FIGURE 8. Mean number of ducks recorded per hour in seven diel periods, based on time-lapse photos taken at a rate of 1/min, 1980.

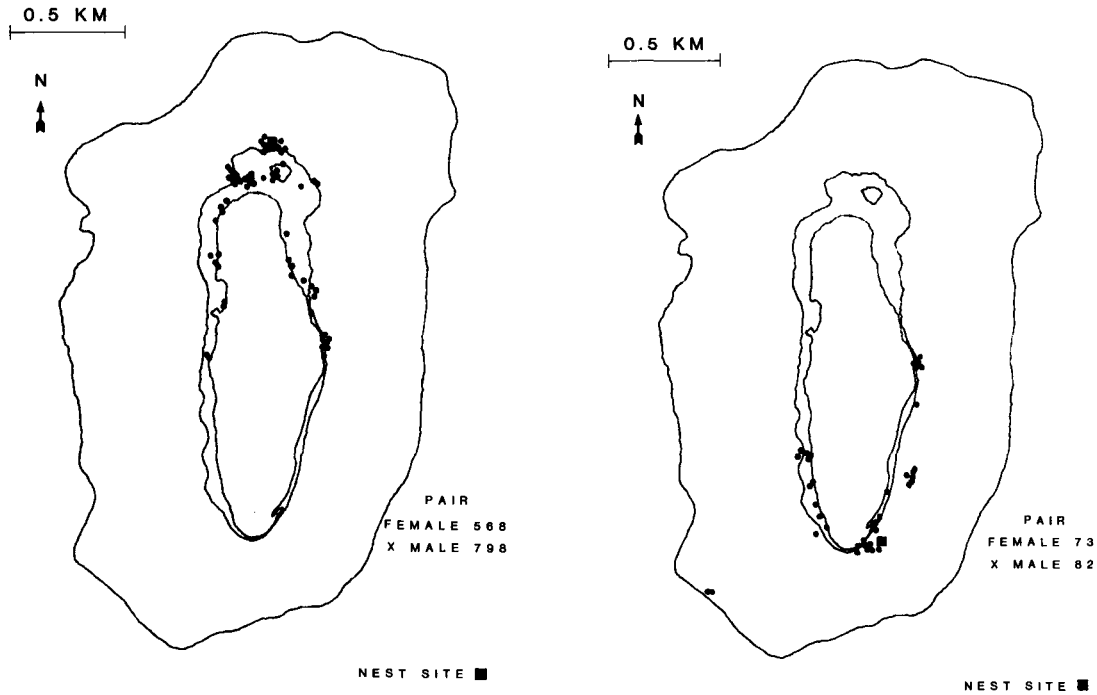

FIGURE 9. Radio fixes on a pair of Laysan Ducks that nested and utilized the northern portion of the lake (left) and another pair that nested and utilized the southern portion of the lake during summer, 1980.

to show the ducks' widespread use of the island. These patterns demonstrated intense use of the lake, and especially the tide gauge and southwest pool areas (Fig. 9), with occasional use of four seashore areas where ducks seemed to bathe: rock ledge, camp beach, log, and south of the southwest pool (Table 4; see Fig. 1 for locations).

The concentration of ducks and other birds along the lake shore near the tide gauge and southwest pool clearly was triggered by a seep of fresh water. Whether ducks could survive without the seep is a moot point, but their intense use of the areas suggests its importance, as is true in other marine waterfowl (Weller 1972). At night, ducks tended to move to the western shore of the lake where invertebrates accumulated because of easterly trade winds. Ducks commonly walked the shoreline and fed in the foamy shallows.

TABLE 4. Duration and activity during three break periods recorded for incubating female No. 916 during one 24-h period.

Time of day	Duration	Location	Activity
15:35–16:54	1 h 19 min	Tide Gauge	feeding
19:19–20:22	1 h 3 min	Camp Beach	bathing
00:47–02:10	1 h 23 min	Southwest pool	feeding

Eight different drakes were radio-tagged during the study. Drakes did not establish exclusive feeding territories, but defended their mates during the prenesting and laying periods while they fed and drank at communal areas. This temporal and mobile territory seemed to be based upon dominance relationships among pairs. Nevertheless, the pairs competed vigorously for limited communal resources such as fresh water.

FOODS AND FEEDING ECOLOGY

During the spring and early summer, adults and ducklings chiefly ate adult brine flies captured on mud flats around the lake, as noted by Fisher (1903) and elaborated by Caspers (1981). Ducks of all ages chased and grabbed flies rising in front of them, and broods spread out and ran side-by-side, perhaps effectively chasing flies into the range of their brood-mates. Brine flies were more numerous in 1980 than in 1979 (Fig. 10), probably because of higher water levels. Nevertheless, the data show dramatic seasonal changes in both years.

Larvae and pupae of *Agrotis dislocata* were probably also an important food (Butler and Usinger 1963, Warner 1963). Adult moths could not be sampled readily, but data for larvae and pupae differed markedly in the two years of study (Fig. 11).

Ducks of all ages sometimes ate muscoid

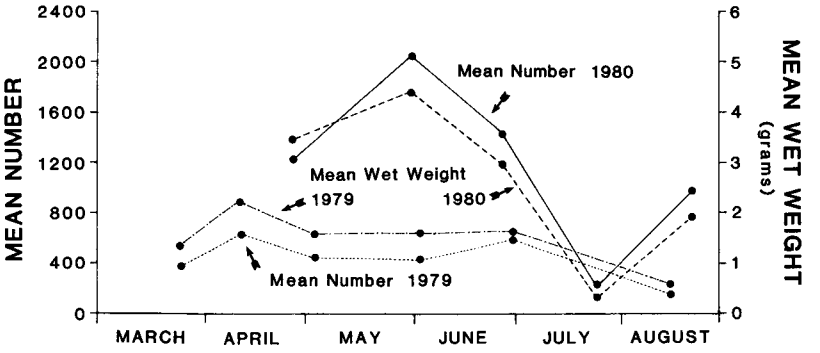

FIGURE 10. Mean numbers and wet weights of brine flies taken in sweep samples at the lake in 1979 and 1980. Numbers were significantly higher in the wetter year of 1980.

blow flies and other terrestrial insects and crustaceans on and around carcasses. In late August 1980, most ducks were "tipping up" to feed on the bottom of the lake in shallow water. Bottom core samples revealed only brine fly larvae and pupae as possible foods. These observations are in agreement with Butler and Usinger (1963), who apparently collected several Laysan Ducks and found *Agrotis* larvae and brine flies. They suggested that ducks feed mainly on *Agrotis* larvae, which are common under *Nama, Boerhavia,* and *Tribulus* plants at night.

Radiotelemetry provided supportive data on feeding behavior. Ducks generally rested during the day and moved to feeding areas in late afternoon and early evening, feeding much of the night. Many ducks went to the tide gauge or southwest pool to drink before proceeding to the feeding areas. Ducks returned to their individually favored resting areas by dawn. Hens tended to nest within their favored daytime resting areas (Fig. 9). Moreover, telemetry showed that some ducks seemed to live almost entirely apart from the lake.

We had no information on winter food supplies, but data on cutworms and brine flies suggested seasonality of production, which may explain the restricted breeding season of these ducks in a subtropical environment. Although invertebrate foods may be less important in the winter, brine shrimp may well be available all year. They were abundant in net samples taken during summer, but birds did not feed in a manner that suggested they were seeking brine shrimp in the lake.

FLIGHT BEHAVIOR AND CAPACITY

Because several species of island ducks are flightless and others are less inclined toward flight than are continental species (Weller 1980), the propensity for flight is of biological

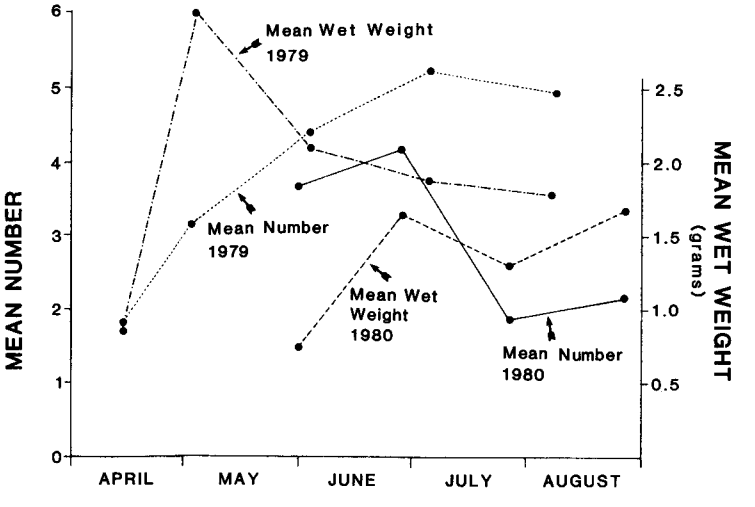

FIGURE 11. Mean numbers and wet weights of *Agrotis* larvae and pupae taken in sand samples in the uplands, 1979 and 1980. Individuals were heavier during the drier year of 1979.

TABLE 5. Data on weights (g), wing area (cm^2), and wing loading in Laysan Ducks. Standard deviation and sample size in parentheses.

	Mean weight	Wing area × 2	g/cm^2
Males	435.17 (35.8) (6)	438.22 (45.5) (6)	0.99
Females	408.40 (39.2) (5)	424.02 (26.5) (6)	0.96

and evolutionary significance. Laysan Ducks regularly fly when they wish to reach the more remote parts of the island. They also walk and run well (Fisher 1903) and are less likely to fly in an escape response than other ducks. A comparison of wing loading in the Laysan Duck and Mallard suggested no decline in wing size in this island duck, relative to its smaller body size. Wing areas and summer, post-breeding weights for six drakes and five hens measured on live Laysan Ducks provide a figure of 0.99 g/cm^2 for males and 0.96 g/cm^2 for females (Table 5). The heavier Mallard ancestor of the Laysan Duck has a still heavier wing loading of 1.11 g/cm^2 according to data presented by Raikow (1973). Such loading is, however, quite light compared to that of diving ducks of similar sizes, such as Canvasback (*Aythya valisineria,* 1.3) or Surf Scoter (*Melanitta perspicillata,* 1.27; Raikow 1973).

Ducks normally have 10 large primaries and a reduced distal one. Flightless Teal (*Anas chlorotis aucklandica*) have lost one or two of the larger primaries, and the loss is not symmetrical (Gadow 1902). Janet Kear (The Wildfowl Trust; pers. comm.) informed us that Laysan Ducks sometimes also lack the full complement of primaries. In 1979, primaries were counted on one wing of 310 Laysan Ducks, of which 229 had only 10 (9 large and 1 reduced) primaries and 81 had the normal complement of 11 (a 3:1 ratio). Birds were not always bilaterally symmetrical in number of primaries. Of 126 additional ducks checked for this feature, only 21 had 11 primaries on both wings, 21 had 10 on the right and 11 on the left, 21 had the reverse, and 63 had 10 primaries on both wings. These data suggest a polymorphism for number of flight feathers, but the ratios do not clarify what the genetic basis might be.

DISCUSSION

STATUS

Past population estimates indicated that the Laysan Duck population fluctuates widely from year to year, but this notion may have been influenced by seasonal variation in behavior of ducks as well as variation in census methods. We conclude that the population now varies about a mean of 500 ducks, and that this number probably represents the present carrying capacity of Laysan Island. Mortality of ducklings and adults, including females probably killed by sexual attack, also indicates that the population may be at the maximal carrying capacity of the island. Limiting influences may be reduced food supplies in the winter and pair tolerance during the breeding period. Whether the species is termed endangered or threatened at this population level is a matter of definition, but it is extremely vulnerable because of its restricted range and such potentially catastrophic influences as introduced predators or herbivores, and tropical storms.

SOME BIOLOGICAL IMPLICATIONS OF ISLAND LIVING

Through years of short-term observations on island ducks, researchers have drawn several general conclusions on their anatomical adaptations, behavior, breeding biology, monochromatism, low mortality and resulting long life-span, permanent pair bonds, increased parental role of males even in northern hemisphere derivatives, and possibly reduced display activity (Lack 1974, Weller 1980). Using a banded population and some radio-marked individuals, the present study demonstrates that only part of these generalities are true, and that Laysan Ducks often behave more like continental species or races than had been supposed. Similar conclusions may be drawn from studies of South Georgian Pintail (*Anas georgica*; Weller 1975a) and Auckland Islands' Flightless Teal (Weller 1975b).

Laysan Ducks **differ** from the ancestral and other continental forms of Mallards by the following:

1) Smaller body size with shorter bill and tail (Weller 1980).

2) Sexual dichromatism is reduced, but again to a lesser degree than occurs in some island ducks. This may reflect more recent establishment.

3) Although data are only suggestive, Laysan Ducks seem long-lived. Several banded birds were 8–12 years of age, which is rare in continental populations.

4) Reproductive rate seems low, based on small clutches, high egg loss, and few young recruited annually. Such a balance between low mortality rate and low recruitment would tend to self-regulate the population at low levels within the present carrying capacity of the island. Although this low reproductive rate also would limit recovery from disasters, the species seems to have accomplished such a comeback in the recent past.

5) They are highly terrestrial and gather food from virtually all habitats on the island.

Laysan Ducks **resemble** continental species in that:

1) Pair bonds are not permanent. Although rate of pair switching is not known for other resident island species, Laysan Ducks stand a 50:50 chance of having a new mate the following year even though the mate of the previous year survives.

2) Pair bonds break after incubation starts but a male may return to his mate if the hen loses a nest or brood.

3) Males do not assist in incubation or care of the young, although they occasionally accompany a brood female.

MANAGEMENT

Although few active management measures promise to influence reproductive success or further population growth of the Laysan Duck, a guardian role is essential with regular population assessments to prevent reduction beyond the level of control. Censuses should be made at least every two years, and should emphasize early night counts along the lake in late spring or early summer. These counts are the least disturbing to the broods and adult ducks and require less crossing of the island, which is destructive to petrel and shearwater burrows. Water levels should be recorded annually, either by an automatic minimum-maximum gauge or by aerial survey of lake size at high-water periods in April. Plant surveys should continue in the event that new exotic plants or those already present dominate native species, which might influence food resources. Laysan Finch numbers should be surveyed to establish the possibility of a reciprocal relationship between this potential egg predator and Laysan Ducks. It is probable that finches are a serious problem only when they are abundant or when human disturbance causes ducks to desert their nests. Protective artificial nest sites should nevertheless be tested to determine whether Laysan Ducks will use them and whether they will inhibit egg predation by finches.

Accidental introduction of other predators must be avoided. Commercial fishing may develop in the area, with a possible increase in shipwrecks, and the danger of the establishment of rats (*Rattus rattus* and *R. norvegicus*). Although the South Georgia Pintail seems to have adjusted to this potential predator, outcomes cannot be predicted. Obviously, the release of mongooses (*Herpestes auropuntatus*) would mean the demise of the Laysan Duck and many other species as well. Regular checks for such eventualities are essential to the maintenance of this delicate island ecosystem.

The major concern for the welfare of the Laysan Duck perhaps is the possibility that blowing sand eventually will fill the lake. Lisianski Island, a still older and smaller island than Laysan, had a lake that has been filled since discovery and exploration. Such a pattern of island evolution on Laysan Island would surely mean the demise of the species. Hence, stabilization of the dunes would be required to prevent this possible event.

If the species' existence is threatened, it may become essential to maintain captive populations that have been regularly mixed with recently captured wild birds from Laysan Island. Mixing of strains from various captives now in zoos may not significantly enhance the genetic diversity of the species because most are derived from the same small population.

In addition, other measures have been attempted or considered by the Fish and Wildlife Service. An experimental planting of 12 ducks was made on Southeast Island in Pearl and Hermes Reef by U.S. Fish and Wildlife Service personnel in 1967. At least one nest resulted, but no ducks have been seen since. Christmas and Washington islands have been considered for additional transplants, but such introductions do not seem to represent an ecologically sound plan for these islands, which have their own endemic faunas.

ACKNOWLEDGMENTS

Funding was provided mainly by the U.S. Fish and Wildlife Service Office of Endangered Species in Hawaii and by a University of Minnesota Graduate School grant to the junior author. Henry Hansen, former Pacific Islands Area Administrator, and Eugene Kridler, former Endangered Species Coordinator of the Fish and Wildlife Service, were instrumental in gaining support for the study. We are indebted to the following persons without whom the study could not have been completed: Ernest Kosaka, Derral Herbst, Craig Harrison, Eric Knutsen, Maura Naughton, and Audrey Newman of the U.S. Fish and Wildlife Service, and David Zellar, Scott Taylor, and Brian Cypher of the University of Minnesota. This is paper no. 13086, of the Scientific Journal Series, Minnesota Agricultural Experiment Station, University of Minnesota, St. Paul and the Station generously funded the color plate.

LITERATURE CITED

ABRAHAM, R. L. 1974. Vocalizations of the Mallard (*Anas platyrhynchos*). Condor 76:401–420.

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. Am. Ornithol. Union.

BAILEY, A. M. 1956. Birds of Midway and Laysan islands. Denver Mus. Nat. Hist., Mus. Pict. 12.

BROCK, V. E. 1951a. Some observations on the Laysan Duck, *Anas wyvilliana laysanensis*. Auk 68:371–372.

BROCK, V. E. 1951b. Laysan Island bird census. Elepaio 12:16–18.

BROOKS, N. C. 1860. Islands and reefs west-northwest of the Sandwich Islands, Pacific. Nautical Mag. 29: 499–504.

BRYAN, E. H., JR. 1942. American Polynesia and the Hawaiian Chain. Tongg Publ. Co., Honolulu.

BUTLER, G. D., JR., AND R. L. USINGER. 1963. Insects

and other invertebrates from Laysan Island. Atoll Res. Bull. 98:1–30.

CASPERS, H. 1981. On the ecology of hypersaline lagoons on Laysan Atoll and Kauai Island, Hawaii, with special reference to the Laysan Duck, *Anas laysanensis* Rothschild. Hydrobiologia 82:261–270.

CLAPP, R. B., AND W. O. WIRTZ. 1975. Natural history of Lisianski Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 186.

DILL, H. R., AND W. A. BRYAN. 1912. Report of an expedition to Laysan Island in 1911. U.S. Dep. Agric. Biol. Surv. Bull. 42.

DWYER, T. J. 1972. An adjustable radio package for ducks. Bird-Banding 43:282–284.

ELSCHNER, C. 1915. The leeward islands of the Hawaiian Group. Honolulu Advertiser, Honolulu.

ELY, C. A., AND R. B. CLAPP. 1973. The natural history of Laysan Island, northwestern Hawaiian Islands. Atoll Res. Bull. 171.

FISHER, W. K. 1903. Birds of Laysan and the leeward islands, Hawaiian Group. U.S. Fish Comm. Bull. 23: 767–807.

GADOW, H. 1902. The wings and skeleton of *Phalacrocorax harrisi*. Novit. Zool. Lond. 9:169–176.

GOLLOP, J. B., AND W. H. MARSHALL. 1954. A guide to aging duck broods in the field. Mississippi Flyway Council, Technical Section Rep. (Mimeo).

KLIMA, M. 1966. A study on diurnal activity rhythm in the European Pochard, *Aythya ferina* (L.), in nature. Zool. Listy 15:317–332.

LACK, D. 1974. Evolution illustrated by waterfowl. Harper & Row, New York.

LAMOUREUX, C. H. 1963. The flora and vegetation of Laysan Island. Atoll Res. Bull. 97:1–14.

RAIKOW, R. 1973. Locomotor mechanisms in North American ducks. Wilson Bull. 85:295–307.

ROTHSCHILD, W. 1892. (Description of *Anas laysanensis*.) Bull. Br. Ornithol. Club 1:17.

ROTHSCHILD, W. 1893–1900. The avifauna of Laysan and the neighboring islands. R. H. Porter, London.

SCHAUINSLAND, H. 1899. Drei Monate auf einer Korallen-Inseln (Laysan). Nossler, Bremen.

SWANSON, G. A., V. B. KUECHLE, AND A. B. SARGENT. 1976. A telemetry technique for monitoring diel waterfowl activity. J. Wildl. Manage. 40:187–190.

U.S. FISH AND WILDLIFE SERVICE. 1982. The Laysan Duck recovery plan. Portland, OR.

VON KITTLITZ, F. H. 1834. Nachricht von den Bruteplatzen einiger tropischen Seevogel im stillen Ocean. Mus. Senckenb. 1:115–126.

WARNER, R. E. 1963. Recent history and ecology of the Laysan Duck. Condor 65:3–23.

WELLER, M. W. 1972. Ecological studies of Falkland Islands' waterfowl. Wildfowl 23:25–44.

WELLER, M. W. 1975a. Ecology and behavior of the South Georgia Pintail *Anas g. georgica*. Ibis 17:217–231.

WELLER, M. W. 1975b. Ecological studies of the Auckland Islands' Flightless Teal. Auk 92:280–297.

WELLER, M. W. 1980. The island waterfowl. Iowa State Univ. Press, Ames.

WETMORE, A. 1925. Bird life among lava rock and coral sand. National Geographic Mag. 48:77–108.

Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minnesota 55108. Present address of first author: Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744. Present address of second author: Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843. Received 3 March 1983. Final acceptance 21 October 1983.

The Condor 86:117

RECENT PUBLICATIONS

Avian Biology. Volume VII.—Edited by Donald S. Farner, James R. King, and Kenneth C. Parkes. 1983. Academic Press, New York. 542 p. $69.50. Ornithology has grown markedly during the past two decades, in depth as well as in its interactions with other sciences. Since 1971, when the first volume in this series was published, some subjects have burgeoned to new importance while others have developed fresh approaches and ideas. Reflecting such progress, this treatise continues to add new volumes (noticed in The Condor 77:521, 85:29) far beyond the number originally envisioned by the editors. The latest contains chapters on avian postnatal development (by Robert E. Ricklefs), the ontogeny of avian behavior (Susan M. Smith), avian ecological energetics (Glenn E. Walsberg), hormonal correlates of behavior (Jacques Balthazart), the biology of avian parasites: helminths (Robert L. Rausch), and the bursa of Fabricius (Bruce Glick). The authors are experts in their fields, and their articles define the present state of our knowledge. As with the preceding volumes, chapters in *Avian Biology* are essential reading in their respective fields for information, ideas, and access to the literature. Illustrated, lists of references at the ends of the chapters, indexes.

Darwin's Finches.—David Lack. 1983. Cambridge University Press, New York. 208 p. $39.50 hard cover, $13.95 paper cover. This classic of evolutionary ecology, first published in 1947, here reappears in an edition with facsimile pages of the original text, tables, maps and drawings. The color plates have been rephotographed from the originals, and the monochrome plates have been either rephotographed or replaced with sharper new versions. Laurene M. Ratcliffe and Peter T. Boag, both at the Edward Grey Institute, have usefully added an introduction putting the book into context. Their extensive notes (with modern references) guide the reader and provide updated information. As they point out, Lack's view on the role of competition has been reappraised. His book nevertheless remains important, thanks to its accurate descriptions of geospizine ecology and behavior, as well as its original, cogent formulation of the adaptive radiation model. Although the present edition is more expensive than mere reprint editions, its cost may be justified to many readers because of the commentary notes.