THE FORAGING ECOLOGY, HABITAT USE, AND POPULATION DYNAMICS OF THE LAYSAN TEAL (*Anas laysanensis*)

by

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ABSTRACT

The Laysan teal, an endangered species, is restricted to a single population on Laysan Island, a remote atoll of the Hawaiian archipelago. Little is known of the Laysan teal's ecology, therefore, I examined food habits, habitat use, and population dynamics. These aspects of its ecology are fundamental to the species management and conservation. I described diel and nocturnal habitat use, home range, and foraging with radio telemetry in 1998-2000. Most individuals showed strong site fidelity during the tracking period, but habitat selection varied between individuals. Mean home range size was 9.78 ha (SE 2.6) using the fixed kernel estimator (95% kernel; 15 birds with >25 locations). Foraging was strongly influenced by time of day: birds spent only 4% of their time foraging in the day, but spent 45% of their time foraging at night. Time activity budgets from the island's four habitat zones indicated that the coastal zone was rarely used for foraging. The birds foraged 42% of the time they spent in the terrestrial zone at night, but foraged only 4-6% of the time they spent there during other times. Fecal analysis and behavioral observations revealed that the Laysan teal is not a 100% macro-insectivore as previously reported, but consumed seeds, succulent leaves, and algae, in addition to adult diptera, diptera larvae and pupae, ants, lepidoptera, coleoptera, and *Artemia*. I concluded that this species exhibits high plasticity in foraging behavior.

I also studied the parameters influencing the Laysan teal's population dynamics. Adult survival is high, but duckling survival on Laysan is low, and is a primary demographic parameter limiting population growth. Estimates indicate the population density was high (between 546-827) from 1991 until August 1993, prior to a population crash that occurred between September and December 1993. The most current population estimate (Sept-Nov 2001) is 444 (SE 181) adults. Additional populations (translocation), along with control of non-native mammalian predators, are needed to reduce extinction risks to the Laysan teal.

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CHAPTER 1: THE LIFE HISTORY AND CONSERVATION OF THE LAYSAN TEAL

Introduction

The Laysan teal, an endangered species, is restricted to a single population on Laysan Island, a remote atoll of the Hawaiian archipelago, (USFWS 1982). Because of the Laysan teal's isolation, few researchers or naturalists have had the opportunity to study its ecology. Only three field studies on the species' biology have preceded the current work (Warner 1963, Moulton and Weller 1984, Marshall 1989). Until now, the species biology in winter has not been studied and little is known about its food habits, habitat use, movements, or population dynamics. These aspects of its ecology are fundamental to management and conservation. In this first chapter, I will synthesize both new and previous studies of the Laysan teal and summarize the following chapters: foraging ecology and habitat use (Chapter 2) and population dynamics (Chapter 3). Additionally, biological observations, my data from 1998-2001 (MHR data), and conservation recommendations that do not appear elsewhere are included here.

Species Description and Taxonomy

The Laysan teal, also known as the Laysan duck (AOU 1998), is unique behaviorally, genetically, and in life history traits. It is a taxonomically distinct species in the waterfowl family (Anseriformes: Tribe Anatini). There are 15 species of dabbling ducks endemic to islands (Weller 1980), suggesting members were originally capable of long-distance dispersal. Once thought to be closely related to the North American mallard group and Hawaiian duck (koloa, *Anas wyvilliana*), new genetic evidence reveals that the Laysan teal's divergence from the koloa/mallard lineage is robust (Rhymer 2001). From a phylogenetic and biogeographic analysis, Johnson and Sorenson (1999) concluded the Laysan teal's ancestor was an ancient member of the mallard clade of E. Asian/Pacific origins.

Laysan teal is a relatively long-lived species (maximum known lifespan 12 years in the wild and 18 years in captivity) with a low reproductive rate (Moulton and Weller 1984, Reynolds and Kozar 2000a). It is primarily insectivorous and is very sedentary and terrestrial for a waterfowl. Having evolved with avian predators instead of mammalian ground predators, the teal are more likely to walk than fly, and when startled they tend to freeze rather than flush. These behaviors make them vulnerable to introduced mammalian predators and exploitation by humans, and may partially explain their extirpation from the main Hawaiian Islands since human colonization.

Laysan teal exhibit a number of morphological adaptations to a largely terrestrial, island existence. They have a shorter middle toe, a disproportionately long femur, and pelvic differences compared to continental dabbling ducks (Livezey 1993). They are also smaller, have shorter wings with fewer primaries, and moderate flight muscle reduction relative to mallards (*Anas platyrhynchos*; Livezey 1993, Moulton and Marshall 1996).

The Laysan teal is a small (38.1-43.2 cm in length) chocolate brown duck with contrasting bi-colored body feathers (USFWS 1982, Moulton and Marshall 1996). It has an iridescent purplish-green speculum and a prominent white eye ring. There is considerable individual variation in plumage. The eye ring is nearly absent on juvenile birds, and becomes more extensive and irregular in adults. Leucistism, or extensive white feathering on the head and neck is common, especially in birds older than three years. The plumage of both sexes looks very much alike, but bill and leg coloring can be used to distinguish sexes. The bill, which is short and spatulate, is olive-green with black blotches along the maxilla in males. Females have a slightly shorter, pale bill with variable black mottling. Both sexes have dull orange legs, although the male's legs typically are brighter (Moulton and Marshall 1996). Morphometric characteristics (wing cord, tarsus, and bill length) are on average slightly larger for males (Moulton and Marshall 1996).

Males are heavier than females, averaging 502 g (SD 46) vs. 485 g (SD 42) respectively, in the non-breeding season (Oct.- Jan.; 2 sample T-test 2.78, df = 221, $p=0.006$; MHR data). Females are heavier than males during the pre-breeding and laying stages, though mass fluctuates significantly between breeding and non-breeding season for females ($N=271$; ANOVA $F=5.32$, $df=1$, $p=0.022$) and males ($N=183$; ANOVA $F=70.2$, $df=1$, $p<0.001$).

Moulton and Weller (1984) found that females with broods were the lightest of the adult birds. Indices of body condition using body mass/wing cord (BC1; Baldassarre and Bolen 1994) indicated that both male and female Laysan teal's condition is better during the non-breeding and pre-breeding months (Oct.-Feb.) and deteriorates during the breeding season (Mar.-July; Table 1). The body condition of individuals recaptured during 1998-2000 also declined (N=68; paired T-test 7.58, P<0.0001): mean BC1 declined from 2.53 (N= 36, SD 0.23) during the non-breeding season to 2.35 (SD 0.20) during the breeding season for recaptured females, and 2.51 (N=32, SD 0.19) to 2.25 (SD 0.16) for recaptured males (MHR data).

Ducklings are precocial and very large relative to adults, weighing 22-30 g newly hatched (Moulton and Marshall 1996). They have dark brownish-yellow plumage with inconspicuous markings. The chin is somewhat lighter; the forehead, lores, and ears are darker. Feathers on the cheeks, breast, belly, wing-patches and around the eye are grayish-yellow. Most ducklings have an eye-stripe, but it is not easily distinguished. The toes and tarsi are olive-brown, with bluish gray webs. The bill is nearly square tipped in appearance distinctly spatulate. Juveniles fledge after obtaining flight feathers at 55-65 days (Moulton and Marshall 1996). Mean weight of fledged juveniles (hatch year birds (HY)) is 407.05 g (range = 361.86-452.24 g; Table 1; MHR data).

Distribution and Habitat

The Laysan teal is a relictual population with the most restricted range of any duck species. The species was extirpated from most other islands of the Hawaiian archipelago after the arrival of humans ca.1500 ybp. Recent subfossil evidence reveals that Laysan teal formerly occurred on most of the major Hawaiian Islands: Hawaii, Maui, Molokai, Oahu, Kauai, and Lisianski islands (Olson and Ziegler 1995, Cooper et al. 1996, Helen James, Smithsonian Institution, *pers. comm.*; Figure 1).

LAYSAN ISLAND

Laysan covers approximately 415 ha., nearly half of which is vegetated. Plant composition changes from coast to interior habitat. Scattered viney vegetation is found near the coast. Further inland are coastal shrubs, bunch grasses, inland shrubs, vines, and matted vegetation. Sedges dominate around a hypersaline lake and adjacent mudflats near the center of the island. Lake salinity varies by season, but is generally 3-4 times that of the ocean. Salt-tolerant species such as algae (*Dunaliella* spp.), brine shrimp (*Artemia franciscana*) and brine flies (*Scatella sexnotata*) dominate the lake ecosystem (Caspers 1981). The lake is surrounded by freshwater and brackish seeps, which also occur at the coast. Although considered among pristine of Hawaiian ecosystems, prior to human contact Laysan Island was quite different than it is today.

Historical accounts from the end of the 1800s described the native flora and fauna in some detail (Schauinsland 1899). Sandalwood trees (*Santalum ellipticum*), native palms (*Pritchardia* sp.), and grasses (*Eragrostis variabilis* and *Cenchrus agrimonioides*) covered the island, but are currently missing or occur in much lower numbers. Seabirds, land birds, seals, and turtles were abundant. After the introduction of rabbits (*Oryctolagus cuniculus*) around 1903, floral and faunal composition changed drastically. The seabirds recovered, but three of five land birds went extinct (the Laysan rail, *Porzana palmeri*; the Laysan millerbird, *Acrocephalus familiaris*; and the Laysan honeycreeper, *Himatione sanguinea freethii*), as did ten species of plants and numerous invertebrates, most of which were associated with host plants that disappeared (Butler and Usinger 1963, Ely and Clapp 1973, Asquith 1994). Humans brought many plant and invertebrate species, notably *Cenchrus echinatus*, a noxious sandbur grass, and ants (family: Formicidae). Prior to the introduction of rabbits, the island's hypersaline lake was deeper and had a coral bottom; devegetation by rabbits from 1903 to 1923 caused drifting sands to fill in the lake and some of the freshwater seeps on the island. A freshwater pond on the southwest side of the island was completely filled with sand (Ely and Clapp 1973).

LISIANSKI ISLAND

Prior to its current range restriction, Laysan teal also occurred on Lisianski Island (Lisianski), approximately 250 km west of Laysan. Early shipwrecked mariners reported ducks on the island but the species identity was unknown (Polynesian 1857). DNA testing of bones from adult and flightless juveniles confirmed that the ducks reported on Lisianski were indeed the species that occurred on Laysan (Olson and Ziegler 1995).

Lisianski is one-third Laysan's size and has a similar geology and history (Figure 1). The island is about 11 m at its highest elevation (Rauzon 2001). The first visitors noted an abundance of beach grasses and a few flowering shrubs, and freshwater was abundant, though sometimes brackish (Polynesian 1844). The vegetation on Lisianski suffered after an onslaught of mice accidentally introduced by a ship sent to rescue shipwreck survivors in 1844 (the same survivors who likely depleted the Laysan teal population there). A sea captain in 1857 noted the near-absence of vegetation, save for a few coarse grasses and small vines, and saw no ducks (Polynesian 1857). What the mice left behind, the rabbits consumed after they were introduced from Laysan around the turn of the century. By 1916, the rabbits had eaten themselves to starvation. Lack of forage killed off the mice as well (Elschner 1925). The flora has mostly recovered and today is similar to Laysan with concentric zones of viney vegetation and bunch grass. *C. echinatus* has become established and is spreading in the native vegetation and along the coast (Starr and Martz 1999, Reynolds and Kozar 2000a).

It is difficult to determine how Lisianski's invertebrate fauna has changed since human contact, but extensive alteration is likely. A recent survey listed 59 arthropod species on Lisianski, only 15 of which were endemic or indigenous to the island. The remaining species were adventive and one was deliberately introduced (Nishida 1999). Reynolds and Kozar (2000a) found *Agrotis* moths and abundant larvae (both serve as prey for Laysan teal) on Lisianski, which were not noted in the 1999 species list.

The interior of Lisianski once contained a swampy lagoon of fresh to brackish salinity, which was sometimes inundated with seawater during the highest tides (Polynesian 1844). Shifting sands destabilized by loss of vegetation filled it. By 1857 nothing of the wetland remained, though freshwater could be found by digging five feet below the surface (Polynesian 1857).

PREHISTORIC HABITAT

The Hawaiian archipelago is an isolated Pacific island ecosystem, with a unique faunal history and late colonization by humans (1400-1600 ybp; Kirch 1982). Anthropogenic predation and habitat change since human settlement have had severe impacts on native birds of islands (Cooper et al. 1996) and Hawai'i provides graphic examples of human-caused extinction and extirpation events. Waterfowl were conspicuous causalities of human impact on indigenous fauna (Williams 1996). Subfossil evidence shows that there are at least eight species of extinct Hawaiian waterfowl representing a unique assemblage of Anseriformes. Hawai`i's extinct waterfowl include the moa-halos, large flightless herbivorous duck species and a large flightless goose (Olson and James 1991). Only three species of endemic waterfowl remain in the islands: the nene (*Branta sandwicensis*), the koloa, and the Laysan teal.

James (Smithsonian Institution, *pers. comm.*) reports remains of adult and flightless juvenile Laysan teal have been found on Hawai`i Island at high elevations including Mt. Hualalai (1244, 1792, 1189, and 1128 m elevation), Mauna Kea and Mauna Loa (1524 m elevation). Remains from lower elevations (61 m) were found near the coast at Hawai`i's South Point. On Maui, remains were found at 825 and 1200 m elevations. On Moloka`i, subfossils were found at Mo`omomi dunes at the coast. Laysan teal bones were found at Barbers Point on Oahu, and on Kaua`i at Poipu, Makawehi and Kealia dunes (Helen James, Smithsonian Institution, *pers. comm.*). Possibly, there was movement between the Hawaiian Islands until the arrival of humans and other terrestrial mammals, when the risk of dispersing increased. That is, perhaps Laysan teal dispersing from natal areas did not survive and eventually the behavior or alleles for dispersal were lost.

The Laysan teal's prehistoric habitat was likely much different from where the species is found today. The distribution of subfossils suggests that the species was a habitat generalist, existing from high altitude forests to coastal wetlands. Additionally, apart from a man-made lake on Kaua`i (created by Polynesian salt-mining), no hypersaline systems exist in the main islands, indicating Laysan teal were not dependent on this habitat.

General Biology and Ecology

HABITAT USE

Prior to the discovery of bones in very diverse habitats on other islands, the Laysan teal were believed endemic to (and specialized for) Laysan Island. Where a species has declined to a single remnant population, the relevance of current habitat is difficult to interpret (Armstrong and McLean 1995). It is important to consider that some aspects of the ecological conditions on Laysan may not be ideal for this species.

Moulton and Weller (1984) found the teal to be very active at night foraging at the lake. Warner (1963), however, described lake use as insignificant during the summer months of his study. I used radio telemetry and behavioral observations to quantify habitat use and activity of the adult teal on Laysan during three breeding seasons and one winter season of 1998-2000 (Chapter 2). Habitat use was characterized by some distinct diurnal patterns and individual variability. Activity budgets and home ranges are described in detail in Chapters 3 and 4. Laysan teal are observed on all parts of Laysan, but typically are hidden in the vegetation and more difficult to observe during the day. Before sunset, the teal emerge from the vegetation and are more visible, especially at the lake.

Surrounding the lake, brackish and freshwater seeps serve as drinking areas for the teal, finches, and shorebirds. Seeps support greater algal growth and organic matter, which attracts higher numbers of feeding *S. sexnotata*. Laysan teal hens used freshwater seeps near the lake edge, ephemeral wetlands, and emergent vegetation (*Cyperus laevigatus, Ipomoea* spp.) as brood nurseries (MHR pers. obs., A. Marshall pers. comm.). Freshwater seeps may be a limiting factor of brood-rearing habitat for ducklings, especially during drought years, or if moisture-rich terrestrial invertebrates are scarce. In 1998, 22 seeps were identified in the interior of Laysan surrounding the lake. During drought conditions, most seeps are below ground and inaccessible to the teal (Table 2).

Waterfowl have suborbital glands that function for salt removal (Schmidt-Nielsen and Kim 1964) and adults drink saltwater; however, hypersaline (>3.3 g/100g) environments can be toxic to young ducklings with underdeveloped salt glands (Wobeser and Howard 1987). Although the adult Laysan teal has an efficient salt gland, the concentration of adults and ducklings at brackish seeps, freshwater seeps, and ephemeral freshwater wetlands implies these sources are important (Lenz and Gagne 1986, Marshall 1989, Moulton and Marshall 1996, MHR pers. obs.). Although freshwater seeps and ephemeral freshwater wetlands appear to be the primary source of freshwater, Laysan teal can take water from a variety of sources. Teal drink dew and rainwater from vegetation (*S. sericea)*, from pooled water on hardpan and mudflats after heavy rains, and from small excavations created around the lake to sample the water table. Laysan teal readily drink water from buckets, camp structures, and watering devices (MHR pers. obs.). The teal also obtain moisture from succulent plants such as *Portulaca* spp. and terrestrial invertebrates, such as lepidopteran and dipteran larvae, which contain over 70% water (Driver 1981, Redford and Dorea 1984).

Foraging

The native plant and arthropod communities of Laysan have changed drastically since the arrival of the first humans to the island (Conant and Roland 1994, Morin and Conant 1998), which likely affected the foraging behavior of the Laysan teal. Observations of the birds in the late 1950s showed that they fed primarily on moth (*Agrotis dislocata*) larvae, and that brine flies were not an important part of their diet (Warner 1963). Studies since then described the brine flies to be an important dietary component (Caspers 1981, Moulton and Weller 1984). Whether this shift in diet was due to environmental conditions on Laysan during the early observations (which were conducted during dry years) or the effect of introduced insects depleting *Agrotis* larvae is unknown.

Diet composition

The Laysan teal is primarily insectivorous, but also feeds opportunistically on seeds, leaves, and algae (Chapter 2.). I observed Laysan teal consuming adult and larval lepidopteran, terrestrial dipteran adults and larvae, *Blatteria* spp. (cockroaches), grass seeds, sedge achenes, and succulent leaves in terrestrial habitats. At the lake, Laysan teal took ephidrid larvae and adults, *Artemia*, algae, sedge achenes, and amphipods.

Foraging Behavior

Laysan teal use a variety of foraging behaviors and foraging substrates (Chapter 2). Foraging behaviors included some tactics typical of dabbling ducks in aquatic environments: dabbling, up-ending, and head-dipping. Other more unusual foraging tactics include, ‘brine fly chasing,’ ‘dry sand filter feeding’, and ‘dive-bomb’ fly-catching. Unique foraging behaviors included tunneling through lake foam to feed on invertebrates suspended in the froth generated during high winds around the lake (MHR, pers. obs.). Laysan teal also take advantage of the carcasses of seabirds (a rich source of flies, larvae, and beetles), and the USFWS camp tents, which trap moths (Warner 1963, Moulton and Weller 1984, Moulton and Marshall 1996, Chapter 2). Historical records note that one duck foraged near the house of the guano mining company's director, looking for moths (Fisher 1906).

Many duck species show notable shifts in diet during breeding. Generally, female dabbling ducks increase their consumption of protein rich foods (animal matter) for egg production (Baldassarre and Bolen 1994). Laysan teal also increase consumption of diptera prior to breeding, and evidence suggests that nesting was initiated when ephidrid (brine fly) densities peaked in 1998, 1999, and 2001 (Chapter 2).

Invertebrate Abundance

Wetland Prey on Laysan

A large number of insect species regularly inhabit areas adjacent to bodies of water and provide an important prey base for waterfowl. Most aquatic dipterans develop as aquatic larvae and pupae, emerging as adults that occupy the wetlands and margins of aquatic habitats (McCafferty 1998). Changes in flooding regimes and lake depth are known to influence the abundance of aquatic dipterans. In particular, wetland flooding triggers the emergence of dipterans, and prolonged dry periods reduce fly emergence (McCafferty 1998). In hypersaline environments, salt-tolerant aquatic plants and arthropod species dominate (*S. sexnotata* and *Artemia* sp.), and can reach very high density.

Many factors are ultimately responsible for producing optimal conditions for the brine flies. Primary production, temperature, and nutrient loads are important ecological variables that influence the life cycle and abundance of wetland flies. Lake depth was a positive predictor of fly abundance because greater lake depths (as a result of increased rain and flooding) reduce salinity, which triggers fly emergence. There is, however, a time lag between flooding and fly emergence. Lake gauge measurements do not consider the direct effect of water levels and salinity on mudflats, thus lake level and fly abundance are not synchronized (Reynolds and Kozar 2000a). On Laysan, dramatic increases in brine fly density can occur, and Laysan teal appeared to initiate breeding after these peaks in 1998-1999 and in 2001 (MHR data, USFWS data; Figure 2).

Artemia (Crustacea: Anostraca) are zooplankters that inhabit high salinity ponds and lakes that are uninhabitable by fish and most other crustaceans (Lenz and Dana 1987). On Laysan, *Artemia* are thought to be an endemic strain of the *A. franciscana* super-species complex (Lenz and Dana 1987, P. Lenz, pers. comm.). *Artemia* are abundant year-round and their distribution is influenced by prevailing winds (Reynolds and Kozar 2000a). *Artemia* are more salt-tolerant than brine flies and have a greater relative abundance at higher salinity. The primary predators on *Artemia* are water birds; however, not all water birds can subsist on *Artemia* alone. Red-necked phalaropes (*Phalaropus lobatus*) at Mono Lake in California, for example, exhibit a preference for brine flies and are unable to maintain their body weight when fed exclusively on *Artemia* (Rubega and Inouye 1994). *Artemia* contain fewer calories and fewer lipids than brine flies (Herbst 1986), which may explain why Laysan teal select brine flies, a more nutritionally profitable prey when available at high density (Chapter 2).

Terrestrial Arthropods on Laysan

The terrestrial arthropod fauna of Laysan is considered the most degraded component of Laysan's ecosystem (Morin and Conant 1998). About 230 species have been previously recorded on Laysan (Nishida 1999), and we established 10 new records during our collections in 1998-2000. At least 80 historically recorded species are native (including 12 Laysan endemics), the rest are introduced (Morin and Conant 1998). Asquith (1994) estimated that 50% of Laysan's native arthropods are extinct. Twenty-four orders of terrestrial arthropods are known from Laysan (Nishida 1999), and nine of these have been documented in the diet of the Laysan teal including Acari, Araneae, Blattodea, Coleoptera, Dermaptera, Diptera, Hymenoptera, Lepidoptera, and Amphipoda (Chapter 2).

Comparisons of arthropod abundance in terrestrial vegetation types indicate that significantly more prey (diptera, coleoptera, adult and larval lepidopteran prey classes) occurs in the viney and mixed vegetation complex compared with bunch grass associations (Chapter 2). Diptera (Sarcophagidae: *Goniophyto bryani*), endemic to the Northwestern Hawaiian Islands and closely associated with seabird die-off, can reach extremely high numbers in mid summer on Laysan (Asquith 1994) providing a terrestrial prey. Native lepidopteran larvae (Noctuidae) in the soil substrate were the most commonly occurring terrestrial prey item found in Laysan teal fecal samples followed by coleoptera (Chapter 2).

In 1984, the first ants were documented on Laysan. Alien ants pose a major threat to endemic arthropods (Holldobler and Wilson 1990, Reimer 1993, Human and Gordon 1997). Habitat destruction and predation by big-headed ants (*Pheidole megacephala*) caused the disappearance of many native Hawaiian insect species, and ants have been implicated in a reduction in numbers of lowland snails (Reimer 1993, Conant and Roland 1994). Ant species found on Laysan are *Camponotus variegatus* (Hawaiian carpenter ant), *Cardiocondyla nuda, Hypoponera punctatissima*, *Monomorium destructor, M. floricola, M. minimum* (little black ant), *M. monomorium*, *M. pharaonis* (pharaoh ant), *Pheidole megacephala* (big-headed ant), *Plagiolepis alluaudi* (little yellow ant), *Tapinoma melanocephalum* (tiny yellow house ant), *Tetramorium bicarinatum* (Guinea ant), *and T. similimum* (Conant and Roland 1994, Nishida 1999). Pharaoh and big-headed ants are particularly aggressive and are suspected to have killed Laysan finch (*Telespiza cantans*) hatchlings on Laysan (Conant and Roland 1994).

REPRODUCTIVE BIOLOGY

Courtship behavior

Courtship behavior occurs most of the year on Laysan, and most adult pair bonds are established by September and October. Monogamous pairing and female-only parental care characterize the mating system of the Laysan teal. Pair bonds break during brood rearing and molt (typically in summer), but if a brood fails early in the breeding season, females usually reunite with their original mates. Mate fidelity within a breeding year based on sightings data was 83% for 35 known pairs. Over multiple years, 69% of mated pairs (n=26) reunited after molt and brood rearing (MHR data).

Nesting

Many ecological features affect waterfowl breeding, such as climate, hydro-period, and temporal availability of suitable food (Baldassarre and Bolen 1994). The

Laysan teal's productivity is highly variable from year to year. The nesting season for the teal on Laysan generally runs from April – July, but reproductive response is flexible according to habitat conditions. Early broods were produced in December 1996 and 2001 (Bernard et al. 1996, Depkin and Lund 2001). Abundant rainfall occurred during those years, and abundant brine flies were recorded in 2000, but were not measured in 1996 (Chapter 2).

Laysan teal are long-lived with a low reproductive rate. Compared to other dabbling ducks, Laysan teal have a smaller clutch size (3.8 eggs) and very large eggs for their body size (Ripley 1960). Large eggs are advantageous at hatching if bigger ducklings are better able to survive under less predictable feeding conditions typical of island ecosystems (Lack 1970). In other species of waterfowl, larger eggs produce larger hatchlings with additional energy reserves (both lipids and larger yolk sacs), presumably reducing risks of starvation and exposure, and providing additional energy for foraging, thereby increasing survival (Ankney 1980, Rhymer 1988, Pelayo and Clark 2002).

The Laysan teal should be considered an 'upland nester', as they typically choose nest sites far from the lake (mean distance 347.6 m from lake and wetlands; range 15-850 m; n=17; MHR data). Females tend to nest in their daytime home ranges (Moulton and Weller 1984, MHR data). Nests made from dead grass, rootlets, and down are well concealed under native bunch grass. Nests often are hidden in grass clumps also covered with vines (*Sicyos* spp.). Of the 26 total nests monitored, 92% occurred in *E. variabilis.* Nests found in other vegetation types included two in *C. laevigatus*, one in *Heliotropium curassavicum*, and one in *I. pes-caprae* (Moulton and Weller 1984, MHR data). Incubation lasts 28-29 days (Marshall 1992a). Nest success in 1999-2000 was 44% (Chapter 3) but previous studies reported much lower nest success (11%) due to egg predation by Laysan finches (*Telespiza cantans;* Moulton and Weller 1984). Egg predation rates may have been elevated due to human disturbance of nests; however, recent studies, using methods modified to prevent nest disturbance, showed 13% of eggs scavenged or depredated by birds, 18% infertile or undeveloped eggs, and 6.5% partially hatched eggs (ducklings died before emerging). The fates of 8% of eggs were undetermined. Hatching success of 61 eggs from 17 nests was 48% (Chapter 3). Our understanding of the nesting biology of the Laysan teal would benefit from additional study.

Brood Care

Laysan teal ducklings are precocial and leave the nest the day of hatching (Marshall 1989). Ducklings follow the hen very closely for the first four days. During this period, hens lead ducklings from upland nesting sites to wetland brood rearing areas. Brood rearing areas are characterized by high invertebrates density, fresh or brackish water, and nearby vegetative cover (*C. laevigatus* or *Ipomoea* spp.; MHR pers. obs.).

Marshall (1989) studied crepuscular and diurnal behavior of broods at the lake (nocturnal and terrestrial behavior was not examined) and found females with ducklings spent most of their time feeding, preening, and stationary. Time of day (0500-2100 hrs) did not affect the frequency of feeding behavior of broods (Marshall 1989). Pre-fledging ducklings were most active during the day. This is in contrast to non-reproductive adults or adult pairs, which rarely fed at the lake during the day (Chapter 3, Marshall 1989). Marshall (1989) found that ducklings spent more time foraging in vegetation in 1987 than in 1986, when they fed more on brine flies, which were more abundant that year. Females brooded most in the morning and evening in 1986. In 1987, ducklings were brooded by the female most often during the last part of the day (1700-2100 hours; Marshall 1989).

Ducklings observed in captivity (Marshall 1992a) demonstrated significant variation in behavior according to duckling age and time of day. Younger ducklings spent more time with the female regardless of their activity, and were more likely to be closer to her. Older ducklings spent more time sleeping, loafing, and engaged in social behaviors. Hens brooded ducklings most often during the morning and evening hours. As with wild ducklings, no significant difference in feeding behavior was observed throughout the day (0500-2100 hrs), but the frequency of swimming and flying (for ducklings >45 days old) increased in the evening hours (Marshall 1992a).

In years with high nesting success, adoption and brood mixing (also called brood amalgamation or creching) is common (Moulton and Marshall 1996, MHR pers. obs.). In 2000, I observed 47% of hens with broods cared for ducklings that were not their own, and 32% of these hens appeared to cooperatively raise broods with other hens (n=112). Parental care such as guarding, brooding, leading, and following was combined or shared between two to four hens with ducklings of different ages. Fifteen percent of hens with broods adopted ducklings that were not their own, but did not associate with other hens. At least 4% of hens observed had their ducklings taken by a more aggressive hen (MHR data).

This level of brood mixing is unusual in dabbling ducks. The high rate of mixing might be explained by kin selection, female body condition, or improved foraging efficiency of larger broods (Eadie et al. 1988). Brooding females are often in poor nutritional condition by the time their young hatch. Female Laysan teal with broods are the lightest of all adult birds, implying it is difficult to maintain normal weight during incubation (Moulton and Weller 1984). The energetic cost of brood rearing could reduce their chances of survival. If they relinquish care of ducklings to a closely related female in good condition, both females might benefit: the mother increases her chances of survival, and the adoptive mother cares for closely related offspring that carry some of her genes. A form of reciprocal altruism could also account for the teal's creching behavior, in which individuals care for others' young with the expectation of repayment in the future (Eadie et al. 1988). On Laysan, conditions might lend themselves to such a system: there is a high probability of meeting the same individual, there is strong site fidelity, birds are long-lived, and individual recognition is probably widespread. Or, perhaps larger broods forage more efficiently, and accepting the ducklings of another hen increases the fitness of a hen's own ducklings. It is typical for 8-20 ducklings of different age classes to form a foraging flock and run through swarms of brine flies (MHR pers. obs.). As clouds of flies rise up from the disturbance, the ducklings snap at them while running with their neck's outstretched (Moulton and Marshall 1996, MHR pers. obs.). Alternatively, brood amalgamation may be a result of crowded brood rearing habitat and not benefit young or adults (Williams 1974, Bedard and Munro 1977, Kehoe 1989). Not all hens adopt ducklings, so creching behavior remains an enigma.

Based on daily sightings of marked hens with new ducklings at the lake (n = 112 broods), 41% experienced complete brood loss during the downy duckling stage, and 23% of these ducklings died during their first week after hatching. Seven percent of marked hens in 2000 produced a second brood after losing the first one (MHR data). Less than 25% of females reared broods to independence during 1977-78 and 1986-87 (Moulton and Marshall 1996). In 1998 only 1% of color banded hens raised broods to independence compared with 33% in 2000 (MHR data). Complete reproductive failure occurred in 1987 and 1993 (Marshall 1989, Moulton and Marshall 1996).

DEMOGRAPHY

Population Size

Laysan teal populations have undergone severe fluctuations this century, from as few as seven to perhaps as many as 688 estimated adult birds (USFWS 1982) although this is believed to be an overestimate (Marshall 1992b). Sincock and Kridler (1977) described the Laysan teal as the most difficult to survey of the four endangered birds of the NWHI. Nocturnal habits and seasonal differences in lake use contribute to the difficulty of estimating population size. In the past decade alone, teal estimates have varied from fewer than 100 to over 600 individuals (Chapter 3). However, most Laysan teal population "estimates" have been direct counts of unknown accuracy. True population estimates were made in 1961, 1979-1980, 1986-1987 and 1998-2001 (Table 3). Previous researchers have determined that direct count and line transect methods are not appropriate for determining population size (Sincock and Kridler 1977, Marshall 1992b). Mark-recapture and mark-resight methods yield the best results. Field studies initiated in 1998 emphasized current methods to estimate population size. Using the Lincoln-Peterson index (Lancia et al. 1994), teal numbers were estimated from the highest total count of the year with 95% confidence limits (Table 3). The most recent Lincoln –Petersen estimate from Oct. 2001 is 459 (391-537) adult Laysan teal.

Sex ratio

The adult sex ratio of Laysan teal is typically skewed towards males (Moulton and Marshall 1996). Male to female ratios in 1979-1980 were reported as 56:44 by Moulton and Weller (1984), who noted female mortality from attacks by unpaired males. Harassment and forced copulation of females by unmated males occur occasionally, but may increase in frequency with the number of extra males in the population. Recent sex ratios determined from resight surveys were very close to unity. The sex ratio estimates were even in 1998, 53:47 in 1999, 52:48 in 2000, and even in 2001 (Table 4). No adult female mortality resulting from trauma was observed from 1998-2001.

Mortality and Survival

Annual survival rate from 1998-2000 was 0.981 (SE 0.005) for adult males and 0.978 (SE 0.007) for adult females (Jolly AGE 5.1; MHR data). Duckling survival, from first sighting to fledging, varied from approximately 0.1 – 0.30 during 1998-2000 (Chapter 3). This level of duckling survival is considered poor for a waterfowl population lacking mammalian predators. On Laysan, there is only one resident duckling predator, the great frigate bird (*Fregata minor*), and the total impact of duckling depredation by great frigate birds is presumed to be minimal. The teal are alert to great frigate birds and ducklings have been observed diving underwater when frigate birds descend or swoop down near them. Duckling survival is the most important variable controlling population growth on Laysan (Warner 1963).

Conservation

The Laysan teal was included in the original Endangered Species List of 1966 because of its small population, limited distribution, and dependence on a fragile island ecosystem (USFWS 1982). The current threats to the species and its habitat are the same as in 1964 at listing and 1982 when the first recovery plan was published (USFWS 1982). Until 1995, the species was believed to be endemic to Laysan Island; however, we now have new information on the distribution of the species. Recent discoveries of Laysan teal remains on other islands provide justification for more effective recovery action and re-establishment of the species to portions of its former range (Cooper et al. 1996).

POPULATION AND SPECIES VIABILITY

In an analysis of Hawai`i's historic avian extinctions, there is a pattern in which species that have large, well-distributed populations are most likely to persist over time (Hu 1998). Once a population shrinks below a certain level, it then becomes vulnerable to stochastic forces, which lead to its extinction (Shaffer 1981). The Laysan teal is reduced to one small population with a limited carrying capacity, and the risks to that population are considerable.

Extinction can be considered a two-phase process. Primary factors can cause initial population reductions at broad spatial scales (Hu 1998). After populations have declined, secondary threats are likely to affect the species, because of its reduced population size and lack of successful dispersal. Island species are especially vulnerable to anthropogenic extinction because of their particular adaptations, such as a longer lifespan with reduced reproductive rate, ecological naivety (*i.e.*, unfamiliarity with new predators), and lower resistance to new diseases (Temple 1985).

The broad causes for bird extinctions have been classified into four main categories (Diamond 1984):

1) harmful species introductions
2) human exploitation
3) habitat loss
4) trophic cascades (secondary extinctions).

The extirpation of Laysan teal from the main Hawaiian Islands was estimated to have occurred 1500 ybp. Harmful species introductions and human exploitation are suspected as the primary factors responsible for their decline. The disappearance of Laysan teal occurs during the appearance of rats in Hawai`i's chronological subfossil record (Burney et al. 2001). The devastating effect of introduced rats on ground-nesting Hawaiian birds is well documented (Berger 1981). Evidence indicates that Polynesian rats (*Rattus exulans*) were more widely distributed than humans were during the period of early human colonization, suggesting that rats were a primary cause for the teal's extirpation (Burney et al. 2001). This threat is still present on most of the main Hawaiian Islands, and additional predators have been added since western colonization, such as black rats (*R. rattus*), Norway rats (*R. norvegicus*), house cats (*Felis catus*), dogs (*Canis familiaris*), and Indian mongooses (*Herpestes auropunctatus*; (Scott et al. 1986). The possibility of secondary extinctions due to an initial extinction seems unlikely if the Laysan teal's ecological niche was that of a generalized understory and wetland insectivore on the main islands.

Once a population is sufficiently reduced or isolated, it then becomes increasingly vulnerable to secondary threats. These threats are primarily stochastic ones, which, acting on a small, localized population, can lead to extirpation. Laysan teal are highly vulnerable to demographic and environmental stochasticity, genetic drift and inbreeding, and catastrophes (Shaffer 1981). All of these threats must be adequately addressed to ensure species viability.

Demographic and environmental stochasticity

Demographic stochasticity is the effect of random events on the reproduction and survival of individuals. It is usually considered a threat only to small populations (Meffe and Carroll 1997). Environmental stochasticity refers to unpredictable events that change vital rates of an entire population, as opposed to individuals. The effects of environmental stochasticity are similar whether the population is large or small (Caughley 1994). Both demographic and environmental stochasticity are important influences on viability of the Laysan teal.

Genetic Considerations

There are two forms of genetic stochasticity that threaten population viability, both of which are usually only dangers to isolated or small populations. The first, inbreeding depression, is the reduction of fitness and vigor by the exposure of deleterious alleles through mating with close relatives. The second, genetic drift, is the loss of heterozygosity due to random, non-adaptive genetic change in isolated populations (Caughley 1994). This loss increases a species' vulnerability to extinction by reducing its ability to evolve in response to new selective pressures.

The susceptibility of island populations to the deleterious effects of inbreeding is uncertain. It is possible that many deleterious alleles have been purged from the population over time and reduced genetic variation will not manifest itself as inbreeding depression. However, preliminary results from studies of individual genetic variation and disease resistance in Hawaiian honeycreepers suggest that birds with greater genetic variation demonstrate higher resistance to an introduced disease, avian malaria (S. Jarvis *et al.* in prep.). The Laysan teal suffered a tremendous bottleneck after their isolation on

Laysan: during the rabbit infestation the population fell to only 12 individuals (7 adults and 5 juveniles; (Dill and Bryan 1912), so the species is likely to have low heterozygosity. However, the impact of this low genetic diversity is unknown. The reduction in fitness from inbreeding depression is often expressed as low reproductive success, reduced hatchability, and reduced disease resistance (Friend and Thomas 1990). We have no indication that the wild Laysan teal exhibit any of these signs; however, a comprehensive study of Laysan teal's breeding biology on Laysan has never been conducted, and nothing is known of their disease resistance.

Catastrophes

Some catastrophes that jeopardize the Laysan teal are hurricanes, global warming, and tsunamis. Disease, environmental disasters, and anthropogenic threats also pose serious risks (*see* Current Threats, *below*). These catastrophic threats can be reduced by: 1) having many populations geographically spaced, to decrease the chance of a catastrophe affecting all populations; 2) having birds on larger islands, such as Kaua`i and Kaho`olawe, that provide more protection from storms and sea level changes; and 3) developing post-disaster contingency plans to restore populations affected by catastrophes.

CURRENT THREATS

The Laysan Island teal population experiences periodic crashes: the most recent was in 1993 when the island suffered a severe drought. Laysan Island is vulnerable to hurricanes, and global warming could exacerbate the frequency and intensity of storms. Alien plant and insect species continue to invade the island, and the likelihood of further introductions is high, as is the chance of contaminants or oil spills washing ashore. Parasite outbreaks are a problem, as are risks of other diseases. All of these threats pose a problem largely because of the limited carrying capacity of Laysan Island and stochastic risk factors to a single population.

MANAGEMENT RECOMMENDATIONS

The strategy to recover the Laysan teal consists of maintaining the population on Laysan and establishing populations on several other Hawaiian islands at levels that are able to withstand negative effects of stochasticity. Populations large enough to tolerate environmental uncertainties will also be able to withstand demographic uncertainties. Additional populations managed for gene flow among them are needed to withstand stochastic threats. Recovery depends on habitat restoration of proposed translocation sites, translocation to other islands, and prevention of harmful alien species introduction to habitats supporting Laysan teal (Sincock and Kridler 1977, Aldrich 1980).

TRANSLOCATION

Habitat restoration and the establishment of additional wild Laysan teal populations on other islands will not only reduce the teal's risk of extinction, but also help restore missing components of the Hawaiian Islands ecosystem. In 2000, a feasibility study was carried out to evaluate translocating Laysan teal to other sites (Reynolds and Kozar 2000a). Restoration of Laysan teal to additional islands may:

1) reduce overcrowding on Laysan during periods of high population density
2) reduce the risk of extinction due to random stochastic events on a single population
3) restore the teal to ecosystems where Laysan teal previously existed
4) act as temporary safeguards in areas free of threats, until habitats on larger islands can be restored.

The Laysan teal is an excellent candidate for translocation. The species is adapted to a very harsh environment, flexible in its foraging behavior, and large enough to carry radio transmitters with high battery capacity (to facilitate monitoring of released birds). In addition, the flight feathers can be trimmed to prevent dispersal from the release site. On a predator-free island, clipping flight feathers would not compromise the teal's survival, foraging, or breeding, and feathers will regrow. With adequate food, water, cover, and protection from mammalian predators, the Laysan teal breeds well in the wild.

Source population

Translocation success is highest with wild-caught animals from high density and increasing source populations (Griffith et al. 1989). These conditions are rare for endangered species, but do occur occasionally in the Laysan teal population. Birds should be removed when populations are increasing. Taking juvenile birds will probably have the least significant impact on the population. Removal of older birds, especially adult females, could cause a decline in the source population by decreasing production. Additional research is needed to determine causes for the low number of females breeding successfully, and the causes for high duckling mortality. Management to increase duckling survival should be explored to balance the effects of removals and to provide more fledglings for translocation.

Transfer population

The best practice to prevent genetic drift within a transfer population is to begin with a sufficient number to minimize drift, and to augment the transfer population regularly with birds from the source population. A minimum of 50 randomly selected founding individuals is recommended to maintain short-term fitness (Frankham 1994). If few individuals are available, selection criteria will depend on how many high-quality birds of the proper age and sex classes are available. Further population supplementation may be required to increase population growth and to improve genetic variability. On Laysan, reproduction is highly variable, and few or no ducklings are produced in some years, so multi-year translocation planning is required.

Selecting and evaluating the release site

For a translocation to be successful, the primary threats that led to the species' initial extirpation must be controlled. Poor habitat quality is the most common reason for the failure of translocations (Griffith et al. 1989, Veitch 1995). In the case of Laysan teal, mammalian predators on the main islands and competitors on the NWHI were the primary limiting factors and will need to be controlled at proposed translocation sites.

Sufficient food, water sources, cover, and breeding sites must also be available at the release location.

Despite the bird's prehistoric distribution in forested areas of the main Hawaiian Islands, only habitats free of mammalian predators should be considered for translocation sites. The negative impacts of predators would greatly increase the risk of reintroduction (Armstrong and McLean 1995, Veitch 1995, Towns et al. 1997). Even the predator-free islands of the NWHI may need additional restoration in the form of pest and weed control, or freshwater seep creation or restoration.

Site visits were conducted to areas where Laysan teal might be reintroduced (Reynolds and Kozar 2000a). Biological characteristics and non-biological suitability features of these sites are summarized in Appendices 1-3. Biological factors include habitat assessment, vegetation characteristics, invertebrate abundance, freshwater, predators, and additional restoration efforts needed. Non-biological features include physical characteristics of the island, logistic feasibility, (i.e., ease of post release monitoring) and infrastructure. Midway Atoll's Eastern Island and Lisianski Island NWR were recommended as the most promising initial release sites, followed by Nihoa Island and Kure Atoll.

Midway Atoll

Midway lies at 28° 12' N and 177° 22' W, approximately 1840 km northwest of Honolulu (Figure 1). The atoll covers 625 ha. and is comprised of two main islands, Sand (467 ha) and Eastern (156 ha), and a smaller islet, Spit Island (2 ha). Like Laysan, Midway Atoll is a National Wildlife Refuge and part of the Northwest Hawaiian Islands Coral Reef Ecosystem Reserve managed by the USFWS.

Eastern Island of Midway Atoll is recommended as the initial experimental release site. Midway is home to permanent USFWS personnel and has irregular air service from Honolulu. Eastern Island has no human settlements and fewer human hazards, thus would be best for the first experimental release. Rehabilitation of habitat on Midway, particularly Eastern Island, is therefore a priority. We recommend a "soft" release, in which birds are gradually acclimated to their environment. This type of release may reduce stress on birds and increases site fidelity, lowering the chance of birds dispersing from the release site (Kleiman 1989). An aviary on Sand Island would be ideal for temporarily housing translocated birds. Laysan teal do well in captivity and should easily adjust to aviary life.

Midway has experienced many non-native species introductions over the years including *Verbasina encelioides* and *C. echinatus*. Efforts are currently underway to control these plants. The invertebrate fauna on Midway Atoll is dominated by exotics. Predatory arthropods such as the big-headed ant may need to be controlled; other introduced invertebrates may provide prey items for the Laysan teal (Reynolds and Kozar 2000a). Fire ants (*S. geminata*) were discovered on Midway Atoll in 2000. A USFWS pilot project to eradicate ants from Spit Island using MAXFORCE toxicant baits appears to be successful (Chris Swenson, USFWS, *pers. comm.*).

In August 1999 and 2001, Ducks Unlimited biologists traveled to Midway to evaluate the atoll as a potential release site for Laysan teal, specifically to evaluate re-creation of wetland habitat to provide a freshwater source (Reynolds and Kozar 2000a; Sharon Reilly, Ducks Unlimited, *pers. comm.*). The water table is less than two meters below the surface in some parts of the atoll, allowing feasible wetland creation. Wetland and vegetation restoration will improve opportunities for successful establishment of self-sufficient, self-sustaining wild populations. Intensive management of Laysan teal at translocation sites, such as providing supplemental food and water or cover, may be required until restoration and revegetation efforts are complete.

Lisianski Island

Lisianski Island is a preferred translocation site. Since Laysan teal existed previously on Lisianski, we know that with adequate management the island can support a population of the birds. Lisianski is Laysan's nearest neighbor in the northwest Hawaiian chain. Loss of plant cover in the mid-1800s resulted in shifting sands that filled the island's fresh water source. This freshwater wetland habitat needs restoration.

Nihoa

Nihoa is considered a preferred translocation site after experimental translocations are made to other islands. At 68 ha, the island is large enough to support a small population of the birds. Native plants and arthropods are abundant. Freshwater seeps occur naturally on Nihoa, eliminating the need to provide water sources or other restoration for Laysan teal. Nihoa is considered the most pristine of the NWHI, so an assessment of the impact of a translocation of Laysan teal there should be conducted prior to translocation (Reynolds and Kozar 2000a). We suspect human impacts to Nihoa (associated with a translocation effort) are the primary risk. Technology for remote or automated post-release monitoring should be explored.

Kure Atoll

Kure Atoll consists of three separate islands comprising 100 ha of land area. The atoll is currently a wildlife sanctuary managed by the State of Hawai`i, which eliminated rats in 1994 and has initiated a weed eradication program to control the spread of *V. encelioides*. The islands support a large number of arthropods and have moderate nesting cover. Freshwater sources could be created to sustain a Laysan teal population there (Reynolds and Kozar 2000a).

Kaho`olawe

Kaho`olawe would be an ideal site for the first translocation of Laysan teal to a main island. Translocation of Laysan teal to Kaho`olawe has already been recommended by the Kaho`olawe Island Restoration Commission (SSRI 1998, Lindsey et al. 1997). Ordnance removal and botanical restoration are underway on the island, which contains moderate nesting cover and a wide variety of arthropods. Ephemeral wetlands exist but need enhancement. Rats have not been seen on the island since 1971, leaving cats as the only mammalian predator. If cats are removed, Kaho`olawe would be a promising release site (Reynolds and Kozar 2000a). Lindsey et. al (1997) acknowledged that cat removal was feasible.

CAPTIVE PROPAGATION

Existing Captive Population

In the late 1950s, 33 teal were removed from Laysan and transferred to captive breeding facilities around the world. Offspring from those birds were used to found a colony at the Pohakuloa Endangered Species Facility in Hawai`i. Seven wild Laysan teal were later added to that flock in an effort to improve breeding. In 1989 captive breeding of Laysan teal was discontinued in Hawai`i. Some birds were shipped to mainland facilities; older birds were euthanized (Reynolds and Kozar 2000b).

Surveys of zoos and private collections in 1999 indicated 211 Laysan teal in 32 collections worldwide, all descended from fewer than 19 founding pairs (Reynolds and

Kozar 2000b). Initially, birds bred well in captivity, but inbreeding depression is suspected of reducing breeding success. Average clutch size for captive broods has decreased from 7.3 eggs reported in 1984 (Marshall 1992b, Moulton and Marshall 1996) to 4.9 in 1999 (Reynolds and Kozar 2000a). Some captive populations may also suffer from genetic pollution: birds have been kept in mixed flocks, and Laysan teal in three facilities are known to have hybridized with a koloa, a northern shoveler (*Anas clypeata*), cinnamon teal (*Anas cyanoptera*) and a wood duck (*Aix sponsa*). Only 15% of facilities surveyed kept pedigrees for their Laysan teal (Reynolds and Kozar 2000a).

The first Laysan teal recovery plan recommended maintaining captive flocks bred to ensure pure strains for eventual reintroduction to the wild (USFWS 1982). Unfortunately, this plan was never realized. Hybridization, incomplete population statistics, and harmful genetic change in captivity make the captive teal and any of their future offspring poor candidates for reintroduction (Reynolds and Kozar 2000b). Genetic change in a captive environment can decrease reintroduction success in two ways: genetic variation can be lost through limited breeding opportunities, or animals become genetically adapted to the captive environment (Frankham 1994). In zoos, natural selection on many features required for survival in nature, such as hunting and foraging abilities, is relaxed. Over long periods in captivity, natural selection acts to maximize fitness in a captive environment, thus the individuals surviving and breeding are those pre-adapted to captive conditions. A review of translocations from 1973 to 1986 found a vastly different success rate between wild-caught (75%) and captive-reared (38%) animals (Griffith et al. 1989).

Disease presents an additional risk to translocating captive-reared birds, especially from mainland facilities. Confinement and mixing with other birds often increases the likelihood of disease transmission in captive flocks (Friend and Thomas 1990). Monitoring, examination, and treatment of birds are essential to protect captive breeding programs. These measures have not been adopted for captive Laysan teal populations, further reducing their suitability as candidates for wild release. The Avian Disease Working Group, an association of captive breeders and veterinarians, rejected the idea of reintroducing captive mainland birds to Hawai`i based on logistical, cost, and quarantine restraints (Cindy Kuehler, Keauhou Bird Conservation Center, *pers. comm.*).

New captive flocks

Midway Atoll and Other NWHI

The flock on Midway should consist of wild-caught fledged juveniles, kept in an aviary in preparation for a "soft" release while habitat restoration is underway. We do not know if fledgling birds will be available for translocation when restoration is complete; therefore, birds should be removed from Laysan between August and November, before restoration is finished and released the following spring. Having Laysan teal ready for release may speed up restoration efforts. If juveniles are available on Laysan, a second cohort can be transferred and released the subsequent autumn.

We believe it is feasible to use captive birds for the NWHI; however, considering the urgency of establishing a new wild population, it would be more expedient, logistically easier, and perhaps would raise chances of success to use wild, parent-raised fledglings from Laysan for other NWHI. It will take years (two to three minimum) before suitable numbers of captive-bred offspring are available for release. Disease risks on the main islands are higher, as are risks associated with transporting birds greater distances from the main islands. Overall, risks are minimized if NWHI translocations are from other NWHI.

Main Islands

Immigration of wild birds from Laysan for the establishment of wild main island populations is also feasible and necessary, but limited in terms of both logistics and the "critical mass needed" for the establishment of large viable populations without depleting the source. If multiple NWHI populations are established and they reach carrying capacity, removal of hatch-year NWHI birds for main island populations would be a good option.

A captive breeding facility, managed for establishing additional wild flocks, may benefit reintroduction efforts and is needed on the main Hawaiian Islands. Eggs taken from Laysan Island could be used to found the captive flock, since eggs are easier to transport than live birds. Wild eggs could be removed, hatched, and raised in captivity, and then released to translocation sites with minimal impact on the source population. However, the advantages of parental learning would be removed. Alternatively, firstgeneration (F_1) offspring from those eggs would be released to found the new wild flocks on the main islands. Captive breeders can minimize genetic adaptations to captivity by specifically managing captive flocks for wild reintroduction. Techniques to minimize genetic changes include reducing time spent in captivity and regularly introducing wild genes. Translocation success can be increased by using only the offspring of wild birds for release and releasing birds into wild or semi-wild habitat temporarily, until suitable habitat within their previous range can be restored (Frankham 1994).

Establishing Laysan teal on the main islands is conditional upon providing adequate predator-free habitat. Introduced predators were most likely the cause of the teal's prehistoric extirpation from the islands, and that threat still exists today. Predator-free habitat can be created by building exclosures, using toxicant baits that target mammals, or through the development of immuno-contraceptives (Innes 1995, Towns et al. 1997, Nelson et al. 2002). Exclosures or barriers including physical and non-lethal electrical barriers and toxicants have been used to control rodents in New Zealand with success (Towns et al. 1997).

CONCLUSION

As our knowledge of the ecology of the Laysan teal grows, we can appreciate the tenacity of a species that has survived the introduction of rabbits to Laysan, drought, disease, and anthropomorphic extirpation from the rest of the Hawaiian Islands. In the subsequent chapters, I discuss food habits, habitat use, and demography of this species within the context of its current habitat.

This study and observations by other researchers indicate that despite its isolation on Laysan and its seasonal preference for brine flies; the Laysan teal is a habitat and diet generalist, perhaps specializing opportunistically. The general requirements of the Laysan teal include vegetative cover, an abundant prey base, a source of water, and the absence of mammalian predators. Extirpations on the main islands were most likely due to introduced mammalian predators, and mammalian predators may be the most important factor limiting their reintroduction. As long as the species is limited to a single population, its extinction risks will be very high. Management should address this risk and the limited carrying capacity of Laysan, although habitat improvements, particularly to brood rearing habitat, may improve duckling survival on Laysan. Experimental translocations are needed now while the population on Laysan is increasing (Chapter 3). Translocation of wild fledged juveniles is the most desirable and feasible method for establishing new populations to reduce the extinction risk considering the species' lack of (successful) dispersal from Laysan Island. Removal of wild eggs and captive propagation may also be applied for conservation with minimal impact on the source population.

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Table 1. Seasonal mass (g) and body condition indices for the Laysan teal 1998-2001 (MHR data).

Month/Yr	Mean mass (SD) Adults		N	N	BC1[1]	BC1	BC2[2]	BC2
	Female	Male	♀	♂	♀ (SD) *N*	♂ (SD) *N*	♀ (SD) *N*	♂ (SD) *N*
Mar98	509.91	498.67	11	9	155.12	144.63	2.63	2.45
	(52.63)	(27.83)			(15.47) *11*	(14.14) *9*	(0.24) *11*	(0.12) *9*
Apr98	477.32	444.32	34	19	136.52	117.96	2.48	2.21
	(51.76)	(31.58)			(16.51) *29*	(8.14) *19*	(0.27) *31*	(0.17) *19*
May98	448.90	450.13	20	16	126.75	119.70	2.32	2.26
	(52.16)	(33.98)			(16.21) *14*	(7.92) *15*	(0.27) *16*	(0.18) *15*
Oct98	486.80	490.50	15	6	139.71	135.82	2.64	2.52
	(20.87)	(72.13)			(5.56) *11*	(27.80) *3*	(0.09) *12*	(0.46) *4*
Nov98	481.71	494.30	28	10	135.67	125.99	2.56	2.48
	(39.53)	(45.19)			(10.16) *13*	(10.54) *9*	(0.19) *14*	(0.20) *9*
Dec98	489.84	528.67	25	24	137.81	139.89	2.58	2.63
	(34.74)	(42.47)			(9.01) *16*	(11.52) *18*	(0.18) *16*	(0.20) *18*
Jan99	515.38	520.19	29	21	147.69	140.73	2.72	2.68
	(33.58)	(45.32)			(6.02) *17*	(8.47) *12*	(0.13) *16*	(0.15) *14*
Feb99	523.47	481.70	15	27	148.51	125.73	2.75	2.42
	(46.32)	(36.21)			(13.44) *8*	(10.31) *17*	(0.25) *9*	(0.17) *18*
Mar99	459.08	434.60	13	10	130.38	111.43	2.37	2.05
	(47.12)	(33.01)			(12.79) *9*	(7.66) *3*	(0.22) *10*	(0.15) *4*
May/Jun 99	452.00	440.83	14	6	121.88	115.65	2.28	2.23
	(55.18)	(24.08)			(11.27) *9*	(5.54) *3*	(0.20) *11*	(0.13) *3*
Mar/Apr 00	468.97	443.57	38	21	130.13	114.17	2.52	2.32
	(40.78)	(26.08)			(11.02) *25*	(7.33) *16*	(0.21) *25*	(0.12) *17*
May00	433.00	429.33	10	12	128.91	109.52	2.50	2.23
	(55.19)	(33.36)			(10.88) *5*	(10.65) *7*	(0.33) *5*	(0.24) *7*
Oct01	436.84	447.00	19	15	112.23	95.16	2.26	2.36
	(33.88)	(25.27)			(26.05) *18*	(47.62) *13*	(0.17) *18*	(0.10) *13*
Total Adult	477.01	475.76	271	196	132.79	121.48	2.48	2.38
	(50.23)	(49.11)			(22.32) *185*	(25.90) *144*	(0.36) *194*	(0.31) *150*
Gravid	486.39		32		135.80		2.52	
	(63.65)				(18.61) *16*		(0.32) *20*	
HY (both sexes)	407.05		44		111.16		2.15	
	(45.19)				(8.96)		(0.55)	
SY	474.04	440.00	22	11	131.29	113.60	2.55	2.33
	(54.32)	(33.62)			(14.94)	(8.15)	(0.26)	(0.11)

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[1] BC1 = body mass/bill length (Harder and Kirkpatrick 1996)

[2] BC2 =body mass/right wing cord (Baldassarre and Bolen 1994)

Table 2a. Salinity and water depth fluctuations of an ephemeral pond on Laysan Island 1998 – 2000.

DATE	SALINITY (g/100g)	WATER PRESENT	SEEP DEPTH (cm)	LAKE GAUGE DEPTH (meters)
02-Nov-98	6.6	Yes	5	2.70
03-Dec-98	9.0	Yes	7	2.64
04-Jan-99	0.6	Yes	27	3.33
03-Feb-99	0.6	Yes	22	3.60
02-Mar-99	3.4*	Yes	24	3.77
05-Apr-99	10.8	Yes	8	3.32
04-May-99	8.0*	Yes	23	3.50
01-Jun-99	10.0*	Yes	13	3.56
14-Apr-00	NA	No	0	3.11
11-May-00	NA	No	0	2.76
8-Jun-00	NA	No	0	2.40
7-Jul-00	7.0	Yes	9	2.27

* Indicates flooding by hypersaline lake

Table 2b. Salinity and water depth fluctuations of Nui Ana seep and Laysan Lake gauge readings on Laysan Island 1998 - 2000.

DATE	SALINITY (g/100g)	WATER PRESENT	SEEP DEPTH (cm)	LAKE GAUGE DEPTH (meters)
26-Mar-98	0	Yes	11	2.06
04-May-98	<1	Yes	15	1.57
01-Jun-98	0.15	Yes	18	1.52
06-Jul-98	0.5	Yes	1	1.22
03-Aug-98	0.4	Yes	1	1.04
07-Sep-98	na	No	0	1.01
05-Oct-98	0.6	Yes	40	2.44
01-Nov-98	0.4	Yes	42	2.70
03-Dec-98	0.4	Yes	46	2.64
04-Jan-99	0	Yes	59	3.33
03-Feb-99	0.2	Yes	68	3.60
02-Mar-99	6.8*	Yes	70	3.77
05-Apr-99	4.6*	Yes	53	3.32
04-May-99	4.4*	Yes	66	3.50
01-Jun-99	6.6*	Yes	56	3.56
14-Apr-00	6.0*	Yes	45	3.11
11-May-00	4.0*	Yes	25	2.76
8-Jun-00	3.6*	Yes	21	2.40
7-Jul-00	1.0	Yes	14	2.27

* Indicates flooding by hypersaline lake

Table 3. Estimates of Laysan teal population size and confidence intervals (95% CI) using line-transect and mark-resight methods.

Years	Population estimate	Methodology	Notes	Birds marked	Reference
1958	594	No CI published; Line transect		n/a	Warner 1963
1961	688 (or 1 teal per .58 ha of suitable habitat)	No CI published Line transect; Est. habitat available = 283 ha	Corrected habitat available for 277 ha = 477 birds[1]	n/a	Warner 1963
1961	544 (404-831)	Lincoln- Petersen Index	Estimates recalculated by MHR in 2001	149	Data from unpub. field notes from R. Walker
1979	462 (432-540)	Lincoln- Petersen Index	April estimate	269-296	Moulton and Weller 1984
1980	510	No CI published. Lincoln- Petersen Index		502	Moulton and Weller 1984
1986	423 (295-551)	Lincoln- Petersen Index	Mean estimate Jun-Aug	200	Marshall 1992a
1987	538 (445-611)	Lincoln- Petersen Index	Mean estimate April-June	270	Marshall 1992a
1998	288 (232-434)	Lincoln- Petersen Index	Adult estimate [2]	100	MHR
1999	292 (263-321)	Lincoln- Petersen Index	Adult estimate [2]	158	MHR
2000	322 (290-354)	Lincoln- Petersen Index	Adult estimate[2]	220	MHR
2001	459 (391-537)	Lincoln- Petersen Index	Adult estimate[2]	260	MHR

[1] New estimates of available habitat exclude the coastal zone

[2] Lincoln-Petersen estimates were calculated from the highest annual count data made during the pre-breeding season

Table 4. Estimates of adult sex ratio using Lincoln-Petersen indices with 95% confidence intervals (CI).

Year[1]	N (surveys)	♂ population estimate	♀ population estimate
Oct. 1998	1	129 (105-154)	130 (111-149)
Jan. – Feb. 1999	3	151 (136-173)	132 (124-144)
Jan.- Apr. 2000	3	252 (218-381)	233 (201-278)
Oct. 2001	1	276 (226-367)	276 (230-360)

[1] Estimates are based on sex ratio resight surveys conducted during the non or pre-breeding seasons.

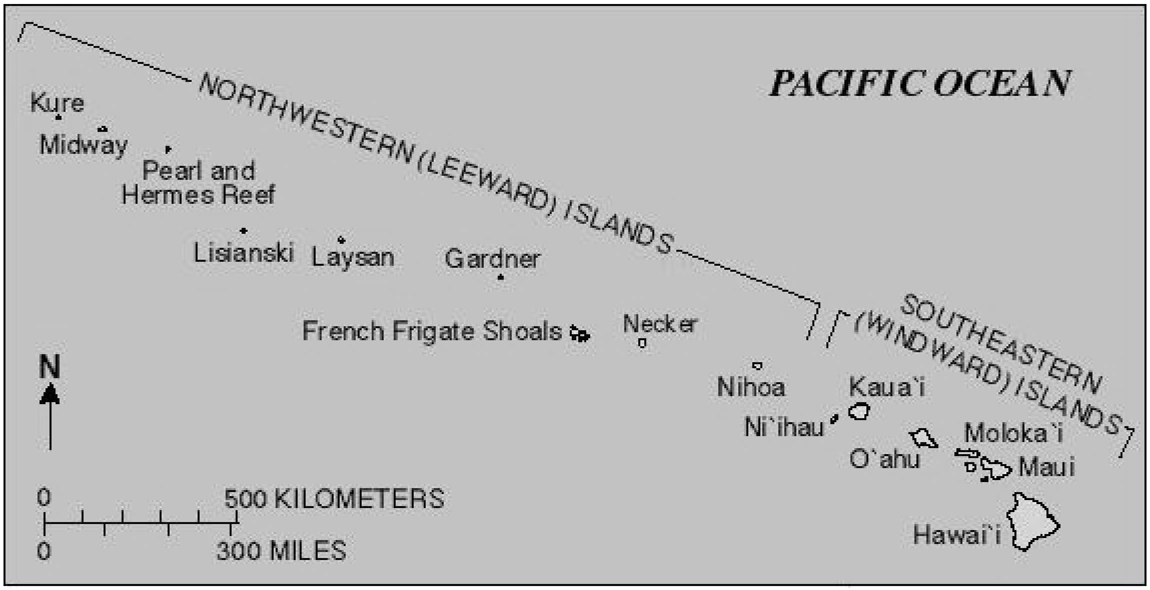

Figure 1. Map of the Hawaiian Islands showing the Laysan teal's known former range; Lisianski, Kauai, Oahu, Maui, Molokai, and Hawaii, current range (Laysan), and site of unsuccessful 1967 translocation attempt (Pearl and Hermes Reef; NOAA 2001).

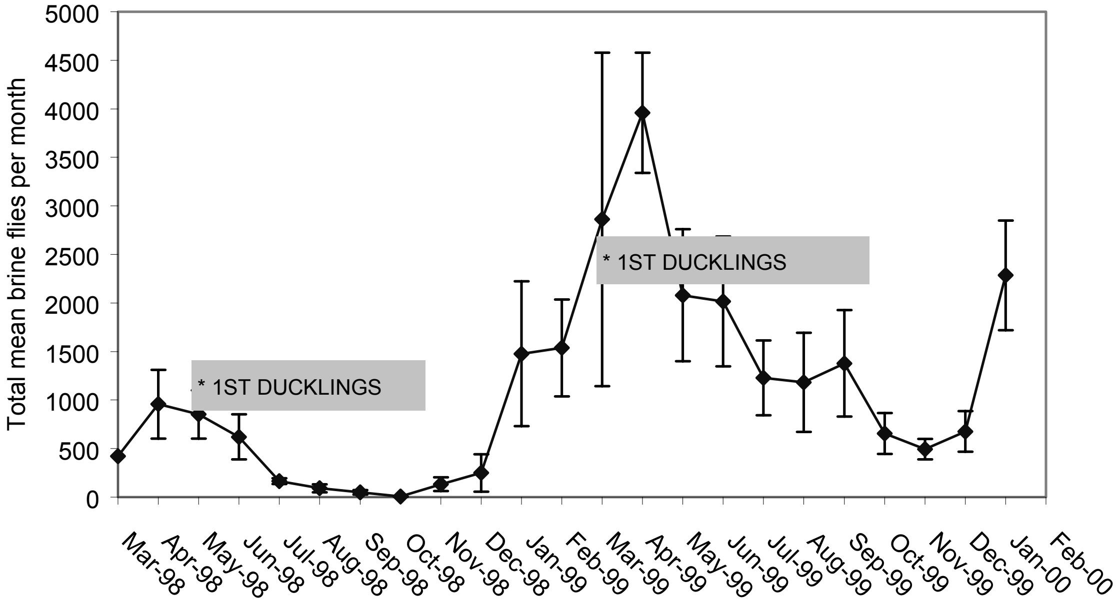

Figure 2. Seasonal brine fly (S*catella sexnotata*) abundance reported as monthly mean with standard error, and first Laysan duckling detections 1998-199

Appendices

Appendix 1. Habitat assessments of possible translocation sites for Laysan teal: Northwest Hawaiian Islands

Island	Size (ha)	Elevation (m)	Annual rainfall (mm)	Fresh water surface	Cover	Mammalian predators	Prey base
Kure Atoll	100	6	1100	Absent	Yes	Absent	Moderate
Midway Atoll	625	5	1121	-	Yes	Absent	Moderate
Sand Is.	467	5		Limited	Limited	Absent	Moderate
Eastern Is.	156	4		Absent	Limited	Absent	Moderate
Spit Is.	2	2		Absent	Limited	Absent	Limited
Pearl and Hermes	30	3	700-1000	Absent	No	Absent	Limited
South East Is.		2		Absent	No	Absent	Limited
North Is.		3		Absent	Yes	Absent	Limited
Kittery Is.		2		Absent	No	Absent	Limited
Lisianski	150	11	700-1000	Absent	Yes	Absent	Moderate
Laysan	415	12	700-1000	Limited-Moderate	Yes	Absent	Seasonally abundant
French Frigate Shoal	26	1-3	700-1000	Absent	No	Absent	Limited
Tern	10			Absent	No	Absent	Limited
East				Absent	No	Absent	Unknown
Necker	18	83	500 -750	Limited	No	Absent	Unknown
Nihoa	68	269	750	Moderate	Yes	Absent	Moderate

Appendix 2. Habitat assessments of possible translocation sites for Laysan teal: the Main Hawaiian Islands.

Island	Size (km2)	Site	Estimated annual rainfall (mm)	Surface fresh water	Mammalian Predators
Ni`ihau	255	Ni’ihau Playas	667	Abundant	Dogs, Cats, Rats
Kaua`i	1574	Wainiha Valley	2000	Abundant	Dogs, Cats, Rats
		Lumaha’i Valley	2500		
		Hanalei NWR	2000		
		Wailua/Opaekaa Valley	1250		
		Hule’ia NWR	1250		
		National Tropical Botanical Garden (Lawa’i Valley)	---		
Oahu	1624	Lualualei	625	Abundant	Dogs, Cats, Rats, Mongoose
		‘Uko’a Marsh	500		
		Kahuku Point	1250		
		La’ie Wetlands	1500		
		Waihe’e Marsh	2000		
		He’eia Marsh	1750		
		Nu’upia Ponds	1250		
		Kawai Nui Marsh	1500		
Moloka`i	660	Moloka’i Playas	250	Abundant	Dogs, Cats, Rats, Mongoose
		Kaunakakai Wetlands	375		
		Kakahai’a NWR	625		
		Paialoa Pond	750		
Lana`i	355	Whole island	250-500	Abundant	Dogs, Cats, Rats
Kaho`olawe	121	Whole island	250-500	Limited	Cats
Maui	1827	Kanaha Pond Sanctuary	500	Abundant	Dogs, Cats, Rats, Mongoose
		Kealia Pond NWR	375		
		Koanae Point	2000		
		Nu’u Pond	1500		
Hawai’i	10458	Pololu Valley	1875	Abundant	Dogs, Cats, Rats, Mongoose
		Waimanu Valley	2000		
		Waipi’o Valley	2000		
		Loko Waka Ponds	3000		
		Ke’anae Pond	3000		
		Koloko Pond	250		
		‘Opae’ula Pond	250		
		‘Aimakapa Pond	250		
		Kona Refuge	---	Limited	

Appendix 3. Summary of assets and liabilities of *preferred* sites evaluated for proposed reintroduction of Laysan teal.

ASSETS	Kure (Green Island)	Midway (Eastern and Spit Islands)	Lisianski	Nihoa	Kaho'olawe	Kaua'i (Hanalei)	Ni'ihau
Size of habitat	Small	Moderate	Moderate	Small	Large	Large	Large
Fresh water	Limited; Creation feasible	Limited Creation feasible	Limited, Restoration Feasible	Available	Limited, ephemeral wetlands and gulches present, wetland enhancement Proposed	Abundant	Abundant
Nesting cover	Moderate	Low, but restoration ongoing	Excellent	Good	Moderate with restoration ongoing	Good	Unknown
Predicted food abundance	Moderate	Moderate to high	Moderate	Good	Moderate	Abundant	Abundant
Logistic feasibility	Limited	High	Moderate	Difficult	Moderate	High	Difficult
Plant foods	Low	Moderate	Moderate	Moderate	Low	Abundant	Unknown
Infrastructure	Some	Good	None	None	Some	Good	Some
Land Management	DLNR Wildlife Reserve	USFWS Wildlife Refuge and Historical Site	USFWS Wildlife Refuge	USFWS Wildlife Refuge	KIRC Cultural and Ecological	USFWS Wildlife Refuge	Privately owned Ranch

Appendix 3. Summary of assets and liabilities of *preferred* sites evaluated for proposed reintroduction of Laysan teal (continued).

LIABILITIES	Kure (Green Island)	Midway (Eastern and Spit Islands)	Lisianski	Nihoa	Kaho'olawe	Kaua'i (Hanalei)	Ni'ihau
Human disturbance or hazards	Minimal	Minimal on East and Spit Islands, Moderate on Sand	Minimal	None	Minimal, after ordnance removal	Moderate	Unknown
Food competitors (mice, predatory alien insects)	Moderate	Moderate	Low	Low-moderate	Low-moderate	Moderate	Unknown
Disease	Low?	Low?	Low?	Low?	Low?	Moderate?	Unknown
Predators	No	No	No	No	Yes	Yes	Yes
Management Required	Freshwater source	1) Revegetation 2) Freshwater source	Freshwater source	None	Predator removal	Predator removal	Predator removal
Management Beneficial	Weed and ant control	Weed, ant, mouse control	Weed and ant control	Unknown	Wetland restoration, mouse control	Upland vegetation restoration	Upland vegetation restoration

CHAPTER 2: THE FORAGING ECOLOGY OF THE LAYSAN TEAL (*Anas laysanensis*) ON A CORAL ATOLL

Chapter 2: ABSTRACT

The Laysan teal (*Anas laysanensis*) is an endangered dabbling duck endemic to the Hawaiian archipelago but currently restricted to a single population on Laysan Island. Little is known of its ecology, therefore, I studied how Laysan teal allocate their time and activity using focal and scan sampling of behavior. I described diel and nocturnal habitat use, diet, and the abundance of select prey with radio telemetry, fecal analysis, and prey sampling techniques in 1998-2000. Foraging was strongly influenced by time of day: birds spent only 4% of their time foraging in the day, but spent 45% of their time foraging at night. Time activity budgets from the island's four habitat zones indicated that the coastal zone was rarely used for foraging, but birds foraged 34-50% of the time when they were in the wetland and lake habitats. The birds foraged 42% of the time they spent in the terrestrial zone at night, but foraged only 4-6% of the time they spent there during other times. A few birds used the camp intensively, and spent 15% of their time foraging on or around camp structures. Most of the daytime hrs were spent under cover in bunch grass, *Eragrostis variabilis* (56%). Laysan teal used a variety of foraging tactics and used a wide range of foraging substrates. Fecal analysis and behavioral observations revealed that the Laysan teal is not a 100% macro-insectivore as previously reported, but consumed seeds, succulent leaves, and algae, in addition to adult diptera, diptera larvae and pupae, ants, seeds, lepidoptera, coleoptera, and *Artemia*. The abundance of adult lepidoptera, brine flies, and terrestrial prey varied seasonally on Laysan. *Artemia* were abundant all year, but Laysan teal preferred brine flies when the flies were abundant. During the 1998 El Nino drought, brine fly and terrestrial prey abundance was low and reproductive success of the teal population was poor. Radio tagged hens (N=13) did not nest during the drought, a period of low prey abundance. Monthly duckling production was positively correlated with brine fly and adult lepidopteran abundance. I conclude that this species exhibits high plasticity in foraging behavior, and should be considered an opportunistic forager specializing on abundant, high energy prey during the breeding season, due to constrained resources on Laysan Island.

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CHAPTER 2: The Foraging Ecology of the Laysan Teal (Anas laysanensis) on a Coral Atoll

Introduction

Anatidae is a widely distributed family, well adapted to wetlands and diverse climatic conditions (Owen and Black 1990). Endemic island waterfowl, several of which are semi-terrestrial, are dramatic examples of the family's pioneering abilities and adaptations to severe conditions (Weller 1980). The Laysan teal (*Anas laysanensis*) is a non-migratory member of the subfamily Anatinae (Tribe: Anatini), endemic to the Hawaiian Islands, but currently restricted to the 415 ha of Laysan Island, an area lacking mammalian predators. The species was previously widespread across the Hawaiian archipelago, but it was extirpated from the main islands during Polynesian colonization and mammalian predator introductions (1400-1600 ybp; Cooper et al. 1996, Burney et al. 2001). The Laysan teal was included on the original U.S. Endangered Species List of 1966 because of its vulnerability to anthropogenic and natural disasters (USFWS 1982). The total estimated population size on Laysan Island has fluctuated between 7-688 adult birds in the last century (Warner 1963, USFWS 1982) and the current estimate is 444 adults (95% CI 391-537; see Chapter 3). With the entire species limited to one small isolated population, the risks to that population are considerable. Once a population is sufficiently reduced or isolated, it then becomes increasingly vulnerable to stochastic threats, which, acting on a small, localized population, can lead to extirpation. Thus, Laysan teal are highly vulnerable to demographic and environmental stochasticity, genetic drift and inbreeding, and catastrophes (Shaffer 1981).

The release of wild birds to establish or re-establish additional populations (translocation), along with control of non-native mammalian predators, are components of ecosystem repair proposed to reduce extinction risks to the Laysan teal (Aldrich 1980, Williams 1996, Reynolds and Kozar 2000a). Translocation of 12 Laysan teal to Southeast Island of Pearl and Hermes Reef was attempted in 1967 to establish a second population (Sincock and Kridler 1977, Berger 1981). Inadequate monitoring of the released birds prevented identification of causes for failure. However, I suspect a combination of factors doomed the effort: poor release methods, marginal habitat, a small number of founding birds, and stochastic factors. A simultaneous translocation of 108 Laysan finches (*Telespiza cantans*) to the same island was successful (Berger 1981).

I am interested in the Laysan teal's foraging ecology, especially as it relates to potential for re-establishment to portions of its former range, which lack the hypersaline ecosystems apparently important to the teal's ecology on Laysan Island (Laysan). Details of plasticity in foraging behavior and range of resource use will enable managers to choose suitable sites for re-establishing populations for conservation, as well as improve our understanding of the species' ecology on Laysan.

Resource use ultimately depends on morphology, behavior, and physiological requirements of the bird. An individual's requirements, availability of resources, efficiency in obtaining those resources, and the occurrence of other individuals or species influence a bird's food and habitat choices (Recher 1990). Food availability to waterfowl can be extremely variable both spatially and temporally, and dynamic or harsh environments can favor opportunistic foraging strategies. One of the foraging tactics adopted by the Laysan teal, its well-known brine-fly chasing sprint (Figure 1), is unusual for a dabbling duck and probably was not important to its foraging ecology prior to the species' severe range contraction to a coral atoll since the other islands lack natural hypersaline ecosystems. A more comprehensive understanding of the foraging ecology of the Laysan teal is needed to better identify its potential niche at other locations within its former range.

Due to the remoteness of Laysan, few researchers have had the opportunity to study the ecology of the Laysan teal. The teal's winter ecology has never been studied previously. Thus, relatively little is known about its foraging ecology on Laysan. Conflicting accounts of the Laysan teal's food habits from previous researchers (Warner 1963, Caspers 1981, Moulton and Weller 1984) add further quandary. Therefore, I studied its behavior, habitat use, and the relationship between abundance of select invertebrate prey and food habits.

STUDY AREA

Laysan has the largest continuous land area of the Hawaiian atoll islands. It is roughly rectangular, approximately 3 km long from north to south and 1.5 km east to west. Laysan lies 1463 km northwest of Honolulu and is accessible only by boat (25º46’ N, 171º44’ W; Figure 2). The island consists of 187 ha of mostly low herbaceous vegetation and 105 ha of an interior lake, and mudflats. The remaining area, approximately 123 ha, consists of unvegetated blowout areas, coastal dune, and beach (Moulton and Marshall 1996). The highest point of the island is 12 m above sea level and coastal reef flats and tide pools surround its perimeter.

Laysan’s lake is characterized by hyper-salinity, high nutrients, and low species diversity. Evaporation frequently exceeds precipitation, and salinity is 2-4 times oceanic salinity (5.8-13.0 g/100g; USFWS data). The lake supports alga and cyano-bacteria growth (*Dunaliella spp*., *Schizothrix sp*.), and dense populations of brine shrimp (Anostraca: *Artemia franciscana*) and brine flies (Ephidridae: *Scatella sexnotata*; Caspers 1981, Lenz and Dana 1987). The *Artemia* feed on phytoplankton and occur throughout the lake’s water column. The larvae of *S. sexnotata* occur in the lake, and feed on aquatic microorganisms and detritus; pupae adhere to the algal substrate on the lake bottom, and the adult flies feed on organic matter occurring in the wetlands surrounding the lake. A subterranean freshwater lens occurs on Laysan and fresh to brackish (0.0 - 3.0 g/100g) water seeps occur in the interior of the island surrounding and within the lake, and at several locations on the coast (Warner 1963). In 1998, I identified twenty-two seeps surrounding the lake. During drought conditions, most of the seeps were below ground and inaccessible to the birds, but during flood conditions, the seeps were inundated by the lake (MHR data). The lake’s maximum depth was 6.5 m. in 1984 (USFWS data), but lake size and depth varies seasonally.

Vegetation associations form concentric bands between the coast and the lake. Scattered ground cover dominated by *Nama sandvicensis* is found closest to the coast.

Moving inland, one finds 1) coastal shrubs, 2) interior bunch grasses, 3) vines 4) shrubs, and 5) wetland vegetation. The dominant species of these vegetation associations are 1) *Scaevola sericea,* 2) *Eragrostis variabilis,* 3) *Ipomoea pes-caprae* or *Sicyos maximowiczii, S. pachycarpus,* or *S. semitonsus, 4) Pluchea indica* and 5) *Sesuvium portulacastrum, Heliotropium curassavicum,* and *Cyperus laevigatus* (Newman 1988). The bunch grass association and the viney association comprise 112.6 ha and 50.8 ha respectively (Morin 1992). Rainfall on Laysan is moderate averaging 79 cm per year from 1992 -2000 (range 38-120 cm per yr; USFWS data).

Laysan is an important nesting colony for several million seabirds. President Theodore Roosevelt declared the island a bird reserve in 1909. Although plumage collectors, seal and turtle hunters, and other mariners visited the island, there is no evidence of human habitation on Laysan before guano miners established a camp in 1893-1909 (Ely and Clapp 1973). A small U.S. Fish and Wildlife Service (USFWS) field camp exists on Laysan today and the island is part of the Hawaii Islands National Wildlife Refuge (NWR) Complex (USFWS 1982).

METHODS:

HABITAT USE

I classified Laysan according to four general habitat zones to describe where Laysan teal forage. The ‘coastal zone’ is defined as the area below the high surf zone, or sparsely vegetated coastal or dune areas on the outer perimeter of the interior bunch grass association. The ‘camp zone’ includes areas within 60 m of man-made structures and storage areas associated with the camp. The ‘lake zone’ includes wetland plant associations, mudflats, ephemeral wetlands, and the hypersaline lake. The ‘terrestrial zone’ includes the island’s interior, excluding wetlands and the camp.

I determined relative habitat use by capturing and attaching radio transmitters to a sample of birds, and systematically tracking the distribution of these individuals among the habitats. I used observational sampling (Altmann 1974, Martin and Bateson 1986) to determine the extent to which time spent in each habitat was devoted to foraging.

Radio tracking

I captured Laysan teal after dark from March–May 1998, Oct 1998-March 1999, May-June 1999, and March-July 2000, using a handheld net of flexible design (Fuhrman Diversified 3/8 x 54 net stick model A1-A/36 DC) and headlamps with Halogen bulbs (Petzel Duo). Some individuals were captured before dark using a noose carpet (Bub 1991). Banding, measurements, and transmitter attachment took place near the capture site and the birds were released within 10-30 minutes. I placed a USGS numbered aluminum band on the tibiotarsus of one leg and applied Darvec (Haggies, Inc.) plastic color-bands, some with alpha or numeric codes, to the other leg and sealed them with laminating glue. Seventy-three birds weighing greater that 400 g were fitted with 6-8 gm radio transmitters (AVM model G3, ATS model 2040) between 1998-2000. I attached transmitters with Tessa™ tape and surgical glue.

I recorded telemetry locations from marked birds between April-July 1998, 1999, 2000, and November 1998-March 1999 using hand held antennas and receivers. Sunrise on Laysan occurs between 0545-0715 and sunset between 1755-1920. Radio tracking was divided into 4 time sessions from approximately 0400–0830 hrs (morning session), 0900-0330 hrs (day session), 1600-2030 hrs (evening session), and 2100-0300 (night sessions). I recorded one location per individual per session. Detection type (signal received and visually confirmed), behavior, habitat use, and time of detection were recorded, and 20 min focal observations of behavior were collected when feasible.

Foraging behavior

I studied the Laysan teal's foraging by observational sampling of behavior in 1998-2000. Continuous focal sampling was conducted on radio tagged and randomly selected birds for approximately 20 minutes. Focal observations of radio tagged individuals were made if time permitted and undisturbed visible detections were possible (i.e. birds were not alert or flushed from vegetation as a result of tracking). Focal animals lacking radio tags were selected randomly within each habitat type: 1) at the lake, a random starting point and direction was chosen, and the first bird encountered of each sex (not of the same pair) was selected as the focal animal. 2) On the coast I randomly selected a direction (clockwise or counterclockwise) to circumnavigate the island, and the first bird encountered was chosen as the focal animal. If a flock of birds was encountered, I rolled dice to determine the focal bird (i.e. 12th bird in flock). 3) In the vegetation, the first bird encountered while radio tracking in this zone was selected. Laysan teal without radio tags were frequently encountered and used as focal animals in the terrestrial zone. 4) In the camp, I walked the camp to coast trail and selected the first bird of each sex encountered. Only one bird per each pair was chosen for focal sampling to ensure independence.

To obtain time activity budgets, focal observations were collected from each habitat type during the same four time-periods defined for radio tracking: morning (2 hrs before and after sunrise: approx. 0400– 0830 hrs), day (approx. 0900-1530 hrs), evening (2 hrs before and after sunset: approx. 1600-2030 hrs), and night (2100-0300 hrs). A digital timer and handheld tape recorder were used to record focal observation data. I used night vision equipment (ITT Night quest 210) for nocturnal observations. Due to the difficulty of observing Laysan teal in the low light conditions of vegetated habitat at night, most observations were made during a bright moon. From radio-tracking, it was obvious that birds were active regardless of lunar illumination. Focal data were transcribed and analyzed using the program OBSERVER 3.0 (Noldus, Inc.).

Additional activity data were collected from the lake zone. The instantaneous activity of individual ducks visible at the interior wetlands, mudflats, and in the lake was recorded with scan sampling techniques (Altmann 1974). I scanned the entire lake zone during an active feeding period beginning one hr before sunset, as determined by Marshall (1989), using a spotting scope (Swarovski HD-AT 80 with 40-60X zoom), 2-3 times per week from April 1998 – Oct. 1999. The direction and starting location of scan sampling was randomly assigned to minimize temporal or spatial bias.

DIET

I collected fecal samples from each habitat to determine what the birds were eating. Analysis of fecal samples is a non-intrusive method for diet determination appropriate for endangered species (Rosenberg and Cooper 1990). Scleritized body parts of most arthropods will pass through the birds' digestive system, and many can be identified. Fecal samples were collected within 5 minutes during banding, radio telemetry, and behavioral observations from the four habitat zones (coastal, camp, terrestrial, and lake) from March 1998 – July 2000, and preserved in 70% ethanol.

Samples were taken from their storage vials, placed in petri dishes, and carefully worked apart using forceps and fine probes for identification. Prey items were viewed under 160-400x with a binocular scope (Leica MZ6) and identified using reference specimens and taxonomic works (Zimmerman 1948, Gepsink 1969, Hardy and Delfinado 1980, McAlpine 1987). The reference specimens were crushed to better resemble the parts found in fecal samples. For all samples, the frequency of occurrence (presence or absence) of prey items in an individual fecal sample was determined. Sixty-two of these samples were analyzed further and identified taxa were counted. Taxa were classified by order and when possible, species and life stage.

PREY ABUNDANCE

I collected data on prey abundance to relate habitat use and diet to the resource base. Availability of prey is the amount of prey useable to birds, whereas abundance refers to the total amount of prey in the environment (Hutto 1990). The availability of prey cannot be sampled directly by researchers in the same manner as by the birds themselves. Therefore, I sampled the abundance of select taxa previously identified as Laysan teal prey (Warner 1963, Caspers 1981, Lenz and Gagne 1986) from foraging substrates: namely soil and vegetation, mudflats and wetlands, and the lake's water column.

Invertebrates of soil and standing vegetation

Macro-invertebrates from soil and vegetation were sampled, during active feeding hrs of the Laysan teal between 2100 and 0100 hrs, at randomly chosen locations along a trail frequented by the Laysan teal. The trail, which meanders from the coast to the interior wetlands, was used to prevent disturbance to nesting birds and damage to the seabird burrows that honeycomb the island. Prior to each sampling session, a random point was selected as the starting location for collecting samples every 5 m at the nearest vegetation clump, alternating to the left and the right of the trail. If a nesting or resting seabird prevented our collecting a sample at a designated vegetation clump, the next nearest vegetation clump was sampled. Each type of vegetation sampled was classified to genus, and later grouped into the following categories: bunch grass (grassy), viney, shrubby, matted vegetation, sedge, or mixed (Table 1). Ten samples were collected twice monthly between May 1998 – Oct 1999 from the soil, and from November 1998 – October 1999 from the vegetation. I intensified sampling and collected invertebrates weekly from both the soil and vegetation from April –July 2000.

Soil samples (360.7 cm^3 each) were sieved for macro-invertebrates (> 1 mm) using three screen sieves (mesh sizes 10, 60, and 230 openings per linear inch; Hubbard Scientific soil profile kit 3196). Invertebrates from sieved soil samples were counted, categorized by order, and released the next day. Unknown taxa were collected and preserved in 70% ethanol for later identification. Ants (Formicidae) were too numerous to quantify using these field methods; thus, only the presence or absence of ants was indicated for each sample.

Vegetation was sampled by expulsion of invertebrates using a stick and ‘beat sheet’ (0.5 m^2; Southwood 1978). Dislodged macro-invertebrates were counted, categorized, and released at the sampling site. Unknown and some commonly occurring taxa were aspirated into vials for later identification and used as reference specimens for fecal analysis. Again, ants were not counted but categorized as present or absent. Additional data collected during each sampling period included time, weather, index of soil moisture, wind speed, and direction.

Adult Lepidoptera in Camp

Adult lepidoptera (moths) were sampled using camp tents as combination interception, shelter, and light traps. This method is similar to that of Malaise trapping (Southwood 1978). I counted, classified, and removed moths trapped in our tent doors every morning before 1000 hr between January – October 1999 and April- July 2000. Artificial light sources and tent sizes varied; therefore, I combined all moth counts to index relative seasonal abundance.

Wetland diptera

I sampled wetland adult diptera using interception trapping (Southwood 1978) at four sites around the lake, twice monthly from April 1998-Oct 1999 and March-June 2001 between 1300-1600 hrs. Water traps were fashioned from 5-gallon bucket lids (660.52 cm^2). Eight water traps per site were placed 5 m apart on the ground at right angles to the lake edge and activated with several drops of biodegradable soap. Microhabitat descriptions, salinity in g/100g, and wind speeds using an anemometer were recorded at sampling sites. Dipterans were trapped for 30 minutes, and then counted using a handheld counter. Sampling was postponed during periods of rainy weather and flooded sites were excluded.

Lake Artemia

Limnological sampling of *Artemia* was conducted using horizontal and vertical plankton net tows twice monthly from April 1998 – October 1999 in Laysan's interior lake. Two methods were used to index *Artemia* distribution and abundance: 1) lake-wide, near-shore distributions and abundance using horizontal tows, and 2) the pelagic region using vertical tows. Horizontal tows were collected in the microhabitat and depth range where ducks were most likely to forage at four locations around the lake: north, east, south, and west sites. A 363-micron (10 cm diameter) plankton net with collecting chamber was used to collect Artemia at selected sampling sites. Horizontal tows were collected while wading at a depth of 15-25 cm using 10-second tows for 2.5 meters between 1000-1600 hrs. Vertical tows were collected at a central location to sample a larger portion of the water column, where *Artemia* abundance is less affected by wind direction. Vertical plankton tows were collected at a buoy in the center of the lake from a small boat at a depth of 5 m at 0900 hrs with a 132-micron plankton tow net (30 cm diameter). Contents of collecting chambers were poured into a white tray and *Artemia* > 1 mm were classified and counted using a hand-held counter. Salinity, wind speed, and direction were also recorded.

STATISTICAL ANALYSIS

The total time activity budget was determined from activity and habitat use of focal observation and radio tracking by each zone and time session. I calculated the product of these proportions, and the daily relative proportion of each time session. The morning, day, evening, and night sessions comprised approximately 20%, 30%, 20%, 30% of the total day, respectively. Percentage data underwent an arcsin transformation and analysis of variance (ANOVA; SYSTAT version 9) to test for difference in activities by time and habitat. I used Tukey's tests for multiple comparisons (Zar 1999).

Data for seasonal invertebrate abundance and weather was subjected to Repeated Measures ANOVA using a mixed model procedure and an autoregressive covariance structure (SAS version 8.2; SAS Institute Inc. 2000). Prey diversity was calculated using Simpson's Reciprocal Index and Shannon-Weiner functions (Krebs 1999). I used non-parametric tests (Kruskal Wallis) for statistical comparisons of fecal prey-part data that lacked a Gaussian distribution (SYSTAT version 9; Zar 1999). Simple and multivariate correlation analyses (Canonical Correlational Analysis) were used to explore the relationship between prey abundance, habitat use, and behavior (SYSTAT version 9). Habitat and prey selection indices are based on ratios of used and available resources (Manly et al. 1993):

$$w_i = \frac{o_i}{p_i}$$

where w_i = Selection indices for resource i

o_i = Proportion of resource used by Laysan teal

p_i = Proportion of resources available in the environment (estimated)

Resource ratio indices, w_i, of 1.0 indicate resources are used in proportion to availability; above 1.0 provide evidence of "selection" and values less than 1.0 suggest "avoidance" or use disproportional to availability. Resource indices are statistically significant if the confidence intervals for w_i do not contain the value 1.0 (Manley et al. 1993). Standardized selection indices also are given by Manley et al. (1993):

$$B\,i = \frac{w_i}{\sum w_i}$$

where Bi = standardized selection index. Values less than 1 divided by the number of resources indicate no preference and values above or below provide evidence of preference and avoidance, respectively. To test the null hypothesis that the Laysan teal are selecting resources at random G-tests were used (Krebs 1999):

$$X^2 = 2\sum_{i=1}^{n} [u_i \ln (u_i/Up_i) + m_i \ln (m_i/(m_i+u_iM/U+M))]$$

where X^2 is the chi-square value (df = n-1), u_i = the number of observations of use per resource i, m_i is number of observations of available resource i, U is the total of observations of use, M is the total observations of availability, and n = the number of resource categories. Standard errors and confidence limits for multiple tests of selection ratios are given by Manly et al. (1993). Assumptions of these analyses are that 1) resource availability and use has been correctly identified, 2) resource availability and use do not change during the study, 3) birds have free access to all resource units and, 4) resource units were sampled randomly and independently.

RESULTS

HABITAT USE

Sixty-two birds were tracked more than twice, 53 were tracked during all four tracking sessions with 10 or more locations recorded, and 11 transmitters detached shortly after attachment. Habitat use varied among radio-tagged individuals (N= 53 birds with 1562 locations). Nine percent of individuals used the camp, 18% used the coast, 96% used the lake zone, and 100% used the terrestrial zone during the periods in which they were radio tracked (Figure 3; also see Chapter 4).

Daily habitat use

Habitat use showed some distinct diurnal patterns (Figure 4; also see Chapter 4**.** I included birds that were tracked at least 2 times in results summarizing daily habitat use (N=62 birds; 1604 locations). The crepuscular tracking sessions (which include the 2 hours before and after sunrise or sunset) were characterized by the most movement, and by use of all habitat zones. At sunrise, many birds were moving from the lake to terrestrial habitat and their movements were largely reversed at dusk. During the dawn session 3% of time was spent in camp, <1% was on the coast, 35% time spent was at the lake zone, and 61% was in the terrestrial vegetation. At dusk, 5% of time was spent at camp, 2% on the coast, 44% at the lake, and 49% in the terrestrial zone. During the day, 5% of time was spent in camp, < 1% of time was spent on the coast, 6% of time was spent at the lake, and 88% of time spent was in the terrestrial zone. Night sessions lacked detections from the coastal zone, had 2% from camp, 59% from the lake zone, and 39% from the terrestrial zones (Figure 4).

ACTIVITY BUDGETS

I categorized Laysan teal behaviors into five activities: active, alert, forage, loaf, and under cover. The "active" category incorporated locomotion, preening, other maintenance behaviors, and all social, courtship, and mating behaviors (Table 2). Descriptions of behaviors are given in Appendix 1 and by Johnsgard (1965). Note that under cover was not a mutually exclusive activity because loafing, incubation, brooding, and other activities also occur while birds are concealed under cover. I analyzed 402 focal observations from 123 males, 251 females, and 28 unknown birds totaling 8511 minutes from 1998-2000. Focal observations are summarized in Table 3. Focal observations of ducklings were not included in this analysis, however reproductive adults and some fledged hatch year birds were included.

Time budget by session

I corrected for the time spent per habitat zone in order to construct a summary time budget for each time of day (N=479 focal observations; Table 5). In the morning, Laysan teal were active 38%, under cover 22%, loafing 18%, foraging 16%, and alert 5% of the time. During the day, birds were under cover 56% of the time and loafed 20% of the time. Loafing is likely to be underestimated since birds under cover are frequently loafing, and are difficult to observe. Birds were active (15%), alert (4%), and seldom foraged during the day (4%). Time spent foraging at dusk was 22%. Birds loafed most before sunset

(31%) and spent only 10% of their time under cover. Laysan teal spent most of their time at night foraging (46%) and active (28%).

Time spent loafing, foraging, and under cover differed significantly by time session ($\alpha=0.05$; ANOVA; Table 5). Significantly more time was spent foraging at night compared with diel sessions (ANOVA $F=18.5$, $df=3$, $p<0.0001$). Time spent under cover was greatest during the day (ANOVA $F=23.8$, $df=3$, $p<0.0001$), and loafing was most common during the day and evening (ANOVA $F=4.33$, $df=3$, $p=0.005$).

Time budget by habitat

I used data from radio tagged birds, making appropriate adjustments for the relative lengths of the four time sessions, to construct time activity budgets for each habitat zone. Foraging was nearly absent in the coastal zone and occurred 44% of the time at the lake zone. In the terrestrial zone, birds foraged 16% of the time, loafed 24% of the time, and remained under cover 34% of the time. Birds were alert on the coast 12% of the time and only 4% in camp despite the frequent human activity. Birds in camp were mostly active (37%), loafing (33%) and foraging (15%; Figure 5; see also Effects of habitat and time of day).

Effects of habitat and time of day

I lack focal observations from camp during the night session, because so few birds used the camp at night. Birds spent time active or loafing around camp on buckets and crates during the morning, day, and evening sessions. In the morning, day, and evening, birds in camp spent, respectively 14%, 11%, and 22% of their time foraging (Figure 6a). Ducks were observed taking moths from tent flys, eating seeds, flies, and succulent leaves and drinking water pooled on the bucket lids around camp. Drinking is included as a foraging activity and occurred frequently in camp where structures tend to trap water (Table 2). Some birds utilized the shade from tent flies and awnings during the day, although this was not included in our definition as “under cover” since their behaviors were visible. Activities in the camp zone did not differ significantly by time of day ($\alpha=0.05$, ANOVA, $df=2$), however time under cover was marginally significant ($p=0.056$) with more time spent under cover during the day.

Nearly all of the coastal zone focal observations are from the evening session because coastal zone visits during other times were rare. Foraging occurred rarely on the coast (>1%; Figure 5). Loafing, preening, antagonistic interactions, courtship, copulation, and bathing were observed at the coast.

The lake zone was an important foraging area during all sessions. Although few individuals without broods used the lake zone during the day (less than 6% of radio-tagged birds), when the teal did visit the lake at midday, 44% of their time was spent foraging. Likewise, birds at the lake in the morning, evening, and night spent 34-50% of their time foraging. Birds were active at the lake zone 33-34% of the time, depending on time of day, and spent 0-14% of the time loafing. Time spent under cover at the lake zone was 12% in the morning when many birds moved away from the lake and took cover after sunrise. Time under cover was 15% during the day but decreased to 2% in the evening and at night in the lake zone (Figure 6b). Most activities did not differ significantly by time of day at the lake zone, with the exception of under cover (ANOVA, F=8.32, df= 3, p<0.001).

I conducted 179 behavior scans at the lake zone between December 1997 and July 1999 totaling 20,446 instantaneous observations (also see Habitat use and prey abundance). Scans before sunset indicated that 29% of birds foraged, 45% were active, 15% loafed and 12% were inactive (standing) or alert. Birds under cover were not visible during instantaneous behavior scans. Behaviors included within the 'active' category are broad, and many would be considered "search-forage" activities during a more intensive focal observation. Thus, the different methods associated with an instantaneous observation preclude direct comparisons with the focal observations. Behaviors within the active category show: 26% of adult birds were engaged in antagonistic, social, and courtship activities; 48% were occupied in locomotive behaviors, 22% were involved in maintenance; and 2% in 'other' activities (Figure 7).

The terrestrial zone was an important foraging habitat for the Laysan teal during the night session, during which period 42% of their time was spent foraging. However, birds spent significantly less of their time foraging in the terrestrial zone during the morning (6%), day (4%), and the evening (5%; ANOVA F=21.66, df=3, p<0.00001). In the morning and daytime, birds spent more time under cover (28% and 62% respectively) than in the evening and night sessions (18% and 19% respectively; ANOVA F=8.32, df=3, p<0.0001). In the terrestrial zone during the day and at dusk, birds spent 21% and 45% of their time loafing respectively, compared to 21% during the morning and 14% at night (ANOVA F=3.77, df=3, p=0.014; Figure 6c).

Total time budgets

I used data from radio tagged birds, making adjustments for the relative lengths of the four tracking periods, to estimate the proportion of the average bird's day spent in each habitat zone. I multiplied the time budget estimates from focal samples for each habitat-time period combination by the corresponding habitat use estimate to construct a summary time budget for each zone. These summaries reveal Laysan teal spent most of their total time budget under cover (26%), active (26%), and foraging (23%). The remainder of their time budget was spent loafing (resting; 20%) or alert (6%; Figure 8).

Foraging behaviors

Laysan teal used a variety of foraging tactics in different habitats and foraging substrates (Figure 9abc; also see Appendix 1). In the camp zone, probing (28%), dabbling (19%), snapping (17%) and drinking (16%) were the most frequently observed foraging behaviors (N= 67 focal observations). Dabbling occurred both in the dry sand at the base of vegetation clumps and from pooled water on camp structures (see substrate use). Foraging tactics at the lake included dabbling (39%), chasing brine flies (18%), and head-dipping and up-ending (9%; N= 276 focals). Foraging tactics in the terrestrial zone were dominated by probing behavior (55%), snapping (19%), and sand dabbling (17%). Tactics of 'picking' (5%) and 'nibble vegetation' (1%) were also observed (N=99 focals).

Substrate use

Laysan teal foraged from a diverse variety of substrate types (N= 442 focal observations). In the camp teal used the camp structures (i.e. tents, buckets, coolers, storage bins) 36%, sand 35%, grass/sedge 16%, and seabird carcasses 4% of the time (Figure 10a). In the lake zone, foraging substrates included the lake edge (24%), the lake (14%), mudflats (13%), matted vegetation (4%) and freshwater seeps (12%; Figure 10b). Birds also foraged on seabird carcasses (3%) and in the wind generated lake foam (8%).

Flies and other invertebrates tended to become trapped and suspended in the lake foam. In the terrestrial zone, viney vegetation (23%), sand (21%), grass/sedge (20%), and seabird carcasses (4%) were used as foraging substrates (Figure 10c). Birds foraging in the terrestrial vegetation, mostly probed substrates at the base of plants, although sometimes birds picked leaves or nibbled the inflorescences of grasses and sedges.

DIET COMPOSITION

Fecal analysis

Laysan teal fecal samples (N=118 samples from 59 females, 53 males, 4 fledged juveniles, and 2 adults of unknown sex) contained prey items in 15 primary prey categories with a mean of 2.9 taxa per sample (range 0-7 taxa per sample). Many samples contained sand and prey parts too finely ground for identification or quantification. Dipteran adults occurred in 47% of the samples, followed by dipteran larvae and pupae (39%), ants (36%), seeds (31%), lepidopteran larvae (25%), and coleopteran adults (23%; Table 6). The number of prey items counted in the 62 fecal samples quantified was 2270 (mean items per sample 36.7; range 0-205). Dipteran adults made up 32% of the total identified prey items counted, followed by *Artemia* (21%), dipteran larvae or pupae (16%), lepidopteran larvae (8%), seeds (8%), and plant fibers (7%; Table 7). Ants made up only 2% of the total items counted despite their higher frequency of occurrence in the samples. Nearly half (47.4%) of the seeds counted were from succulent plants, *Portulaca spp*., found in the terrestrial zone. Other intact seeds identified in fecal samples included *Cyperus laevigatus, Fimbristylis cymosa* and *Mariscus pennatiformis.* An unpublished analysis of fecal samples (n=28) collected from birds at the lake during the summer of 1985, showed higher occurrence of *Artemia* and *Blattaria*, fewer ants, and no seeds (Lenz and Gange unpublished data; Table 6)

I tested for differences in the frequency of occurrence between the composition of prey items collected from the lake zone (N= 45 fecals) and the terrestrial zone (N=30 samples; Figure 11). I lacked data on the time spent in the zone prior to the collection of fecal samples or the food passage rates for these species, therefore variation due to birds recently foraging in other areas was expected. Significant differences (α= 0.05) in the occurrence of taxa were found for ants, lepidopteran larvae, and seeds, which occurred more frequently in samples collected from the terrestrial zone, and adult dipterans, which occurred with greater frequency in the samples from the lake zone (Table 7). *Artemia* occurred in only 14 samples from the lake and terrestrial zones, and its frequency of occurrence did not significantly differ between them. However, the number of *Artemia* counted was significantly higher in the lake zone samples than the terrestrial samples (Kruskal Wallis H=4.72, p=0.030). *Artemia* are found exclusively in the lake and lepidopteran larvae typically are absent from the lake zone.

Behavioral observations

Observations indicate that adult and larval lepidopteran, terrestrial dipteran adults and larvae including maggots from seabird carcasses, *Blattaria* (cockroaches), grass seeds *Sporobulus* sp., sedge achenes *Fimbristylis cymosa*, and succulent leaves from *Portulaca sp*. are taken while foraging in the terrestrial habitat. Laysan teal in the lake zone ate algae and sedge achenes (*Cyperus laevigatus*). Because of the difficulty in observing the consumption of small dietary items in dabbling ducks, diet from focal observations could not be reliably quantified. Nevertheless, I suspect that succulent leaves, algae, and adult lepidopteran, which were well represented in foraging observations (Table 9), may have been under represented or not identified in the fecal samples.

INVERTEBRATE ABUNDANCE

Camp Zone

Adult lepidoptera from tent trapping showed a strong seasonal pattern with high abundance in summer both 1999 and 2000 (Fig. 12). Fewer moths were trapped during the 1998 El Niño drought year and the seasonal pattern was less pronounced. There was a significant effect of month on adult lepidopteran abundance (Repeated measures ANOVA, F=29.28, df=22, p<0.0001). Moth abundances in tent fly doors reached 1345 in one day (12 June 1999). Two species identified from camp tent trapping, *Agrotis dislocata* and *Agrotis evanescens,* were consumed by Laysan teal.

Coastal Zone

Laysan teal rarely foraged on the coast (see Time Budget). Therefore, I did not analyze invertebrate abundance in the coastal zone.

Lake Zone

Brine fly abundance was highly seasonal (Figure 13) and abundance varied significantly by month (Repeated Measures ANOVA, F= 9.263, df=21, p<0.0001). Brine fly abundance increased sharply after December in 1998 and 1999, and seasonal peaks occurred in the spring months (April and May) of 1998 and 1999. Very high brine fly densities occurred in April of 1999 with a maximum density of 4037 flies per bucket lid or 6.11 flies/cm^2. Data from February–March of 2000 is incomplete, so data after February 2000 were excluded from seasonal analyses using repeated measures. However, for the months where data were collected (April-July of 1998-2000), I pooled fly count data by year and compared yearly differences in brine fly abundance. Significant differences existed for brine fly abundances between years (ANOVA F=38.21, df=2, p=0.0001). Pairwise comparisons indicated that 1999 differed significantly from 1998 and 2000.

Artemia (sampled with vertical tows) was typically abundant year round (Figure 14) and showed no seasonality. *Artemia* abundance did not differ significantly by month (Repeated Measures ANOVA, F= 0.828, df=11, p=0.57). Lake edge horizontal tows showed that the distribution of *Artemia* was influenced by wind direction. Thus, although the abundance of *Artemia* did not vary significantly by season, the distribution of *Artemia* was influenced by seasonal trade winds. Strong northeasterly trade winds concentrated *Artemia* in the southwestern edge of Laysan's lake during the months of November and December 1998 (Figure 15).

Terrestrial Zone

The most abundant soil invertebrates captured during sieve sampling were lepidopteran larvae (24%), gastropods (19%), coleoptera (14%) and amphipods (9%) (N=487 sieve samples; Figures 16). In the field, I could not easily distinguish between 1-3 mm live snails and snail carcasses (*Tornatellides sp*. unconfirmed). Dead snails are likely an unattractive prey item to Laysan teal, so the abundance of snails in sieve samples is an overestimate of available live prey. The most abundant invertebrates counted in standing vegetation (N=367 samples) included coleoptera (37%), arachinida (19%), lepidopteran adults (15%) and diptera (12%; Figures 17). The frequency of ants (presents or absence) per sample was 36% of the soil and 46% of the standing vegetation samples.

Invertebrate abundance for the two terrestrial substrates sampled, soil (N = 487) and standing vegetation (N=367), was analyzed separately to explore differences in composition and abundance of invertebrates among grassy, viney, and mixed substrates using Kruskal Wallis tests. Soil samples within the grassy (N=302), viney (N=101), and mixed vegetation (N=84) were tested for differences in the abundance of taxa captured between vegetation types. Significant differences were identified for lepidopteran larvae (H=26.712; df = 2; $p<0.0001$), gastropods (H=6.597; df=2; p=0.037), 'other' combined taxa (H=7.279; df=2; p=0.026), and coleoptera (H=7.562; df=2; p=0.023). Lepidopteran larvae were more abundant in soil of the mixed and viney vegetation than the grassy vegetation. Gastropods were more abundant in the grassy vegetation's soil, 'other' invertebrates were more abundant in the mixed vegetation soil, and coleoptera in the viney vegetation soil.

Invertebrates sampled in the standing vegetation (grassy N=231, viney N=67, and mixed vegetation N=69) showed significant differences for coleoptera (H=68.47, df=2, $p<0.0001$), arachnida (H=51.91, df=2, $p<0.0001$), diptera (H=53.86; df=2; $p<0.0001$) and adult lepidoptera (H=13.09; df=2; p=0.001). Pair-wise comparisons indicated coleoptera were more abundant in the viney standing vegetation, arachnida in the grassy vegetation, diptera in the viney vegetation, and adult lepidoptera in the mixed and viney vegetation.

The diversity of potential invertebrate prey sampled from grassy, viney, and mixed vegetation types were compared from soil samples using Simpson's reciprocal index (N_2) and the Shannon-Weiner function (H'), and the number of equally common taxa were calculated for each vegetation type (Table 10). N_2 varies from 1 to *s* where *s*= the number of total taxa. H' typically ranges from 0 to 5, with 5 indicating high diversity. Soil samples from each vegetation type indicated that species diversity increased along a continuum from the grassy *Eragrostis* (N_2 = 4.79; H' = 2.73), to the viney *Ipomoea/Sicyos* (N_2 = 6.19; H' = 2.97), to the mixed vegetation (N_2 = 7.57; H' = 3.18), indicating that both prey diversity and prey abundance are highest in soils from the viney and mixed vegetation types.

Invertebrate diversity from standing vegetation types indicated that diversity was highest for mixed vegetation (N_2 = 5.50; H' = 2.78), followed by *Eragrostis* (N_2 = 4.79; H' = 2.73) and *Ipomoea/Sicyos* (N_2 = 1.93; H' =1.41; Table 10).

I evaluated seasonal variability in prey abundance, the effects of vegetation type and the interaction term of 'month x vegetation' from June 1998-Oct.1999, and Apr. 2000-July 2000 for soil sieves, and Nov. 1998-Oct. 1999, and Apr. 2000-July 2000 for standing vegetation (Figure 18 and 19). Mean prey abundance of soil invertebrates from sieves (all taxa pooled) varied significantly between months for 1998-1999 (Repeated Measures ANOVA; F= 5.02, df= 15, p<0.0001). Vegetation type was marginally significant (F=2.42, df=4, p=0.059), and month x vegetation showed a significant interactive effect (F=2.54, df=24, p=0.0002). Prey abundance did not vary among months during April-July 2000 (F=0.98, df=3, p=0.41), but again vegetation had a significant effect on soil prey abundance (F=9.51, df=4, p=<0.0001), and there was a significant month x vegetation interaction (F=3.63, df=3, p=0.0016).

The same statistical procedures were applied to examine invertebrate abundance on standing vegetation. Again, prey abundance was strongly affected by month in 1998-99 (F=6.31, df=11, p<0.0001), but not by vegetation type (F=0.73, df=4, p=0.57). In 2000, month did not effect prey abundance (F= 1.25, df=3, p=0.29), but vegetation type did (F=41.43, df=4, p<0.0001), and there was a significant month x vegetation interaction (F=3.14, df=7, p=0.005; Figure 19).

RELATIONSHIP TO RAINFALL AND BREEDING

Pairwise comparisons indicated that in 1998, an El Niño drought year, annual rainfall on Laysan was significantly less than in 1999 and 2000 (H=8.45, df=2, p=0.015). The monthly pattern of rainfall also differed significantly during the 3 years (Repeated Measures ANOVA F=1.89, df=35, p=0.0015; Table 11).

Annual variation in rainfall, abundance of brine flies, and prey invertebrates were positively related for the three years. Breeding success was higher in years when rainfall and prey abundance was higher (Figure 20). Monthly brood production (new brood sightings) had a positive relationship with brine fly abundance (Pearson correlation coefficient = 0.77, $p<0.001$) and moth abundance (Pearson correlation coefficient = 0.64, $p=0.005$) during 1998-1999 (Figure 21).

Resource Selection

Resource selection by radio tagged birds was evaluated using selection indices analysis (Manly et. al 1993). Habitat availability is based on estimates by Morin (1992) and new calculations of island area based on satellite imagery (IKONOS 18Dec2001; Table 4).

Behavior and habitat use

I compared the activities (use) of the visually confirmed radio-tagged birds (n= individuals; 258 locations) and the availability of three terrestrial vegetation types using a chi-squared log likelihood statistic. Sample sizes were too small for analysis of activity-habitat preferences per individual, therefore I pooled location data. Foraging occurred more frequently in the mixed and viney vegetation compared to the grassy vegetation indicating that foraging habitat was not randomly selected ($X^2=21.614$, df =2, $p<0.0001$). Bunch grass habitat was used for cover more than would be expected by chance ($X^2=6.184$, df =2, $p=0.044$). No significant differences were found for the other activity categories between vegetation types: active ($X^2=1.221$, df =2, $p=0.54$), alert ($X^2=2.65$, df =2, $p=0.27$), or loafing ($X^2=5.07$, df =3, $p=0.08$; Fig. 22).

Prey selection

I compared abundance of invertebrates from two terrestrial foraging substrates, soil and standing vegetation, to the abundance of invertebrate prey items counted in fecal samples collected from these habitats for the same period. An assumption of the analysis, that available food resources are constant during the study period, is difficult to satisfy for most studies (Manly et. al 1993), and was not met for this study because some taxa showed seasonal variability (see prey abundance). In this case, prey selection inferences are made with respect to “typical” conditions during the study period (Manly et. al 1993). I excluded aquatic prey (*Artemia*) and diptera that could be from either wetland or terrestrial habitats, but included diptera identified as terrestrial. I tested the hypothesis of equal use with a chi-squared log likelihood statistic. Results provide evidence of non-random prey use in both the soil substrate (X^2 =341.517, df =7, P<0.0001), and standing vegetation (X^2 =77.54, df =4, p<0.0001; Table 12). Laysan teal selected the most abundant invertebrates in some cases but did not use other abundant taxa. In the soil substrate, Laysan teal preferred two of the most abundant invertebrates, lepidoptera larvae and coleoptera. Amphipods were selected in proportion to their abundance and small gastropods (*Tornatellides sp*.), isopods, and arachnids were not consumed or were used in disproportion to their abundance. I did not distinguish between live, dead, or aestivating snails and suspect many were dead, and unlikely prey. In the standing vegetation, Laysan teal preferred the most abundant taxa: coleoptera. Laysan teal appeared to avoid arachnids, however sample sizes of resource use were too low to be reliable (Table 11).

HABITAT USE AND PREY ABUNDANCE

The proportion of time spent in each habitat zone by radio tagged birds was explored during the months when both tracking and prey sampling occurred. The proportion of time spent in the camp zone was positively related to the monthly mean adult lepidopteran abundance in camp (Pearson correlation coefficient = 0.84, p= 0.013; Table 13). No other significant correlations were found.

Twenty-one percent of the total foraging effort at the lake the hour before sunset was dedicated to feeding on the brine flies. Brine fly foraging tactics observed during scan sampling included chasing after adult brine flies at a run, and snapping at flies while walking, standing, or swimming. Other feeding behaviors at the lake, not specific to foraging on brine flies, included dabbling, drinking, head dipping, carcass probing, up-ending, and others (also see foraging tactics). The proportion of ducks foraging on brine flies varied seasonally. Between July and November 1998, no foraging on brine flies was observed, whereas from March to May 1999, the teal spent greater than 50% of their foraging effort on brine flies, suggesting selection for brine flies only when they are very abundant (monthly mean >1000 flies per transect; Figure 23).

The brine fly foraging behavior was strongly correlated with mean monthly brine fly abundance (Figure 21; Pearson's correlation coefficient = 0.903, p < 0.0001), whereas the proportion of total birds foraging (all foraging behaviors) was not correlated with brine fly abundance (Pearson's correlation coefficient = 0.410, p= 0.115).

DISCUSSION

The response of a bird to its environment and the resources it uses may change in response to weather, change in abundance or availability of resources, and differing physiological requirements depending on the phenology of the species (Recher 1990). For example, its habitat requirements may differ during laying, brood rearing, or molting. Breeding on Laysan occurred at the peak of brine fly abundance during 1999 and 2001; and brood production was positively correlated with brine fly and moth abundance in 1998-1999. This suggests breeding occurs during periods of high prey abundance and that both breeding and foraging are opportunistic.

Specialization may occur because few resources are available in a particular environment or specific characteristics of the organism may constrain its diet (Recher 1990). The diet of the Laysan teal prior to its isolation on a coral atoll was likely to be quite different from its diet today. Adult and duckling Laysan teal bones were found in a diversity of habitats including coastal wetlands and high elevation forests far from water (Cooper et al 1996). From this, I speculate that the species was a generalist, and that it fed in the leaf litter of the forest floor and in coastal wetlands. Indeed, observation of the Laysan teal foraging in the terrestrial vegetation at night are reminiscent of feral pigs (*Sus scrofa*) in Hawaii's rainforest moving the substrate around with their snouts in search of earthworms and other food. Ideally, ancient stable isotope techniques on subfossils could be used to learn about the Laysan teal's diet prior to its restriction on Laysan.

The conflicting reports about the foraging ecology of the Laysan teal on Laysan are likely due to limited observations from short visits to the island and varying environmental conditions (Marshall 1989). Introductions of alien species such as rabbits (*Oyrctolagus cuniculus*), skinks, ants, and other arthropods have had unknown impacts on the prey base and diet of Laysan teal. The native plant and arthropod communities of Laysan have been severely degraded in the last century (Conant and Roland 1994, Morin and Conant 1998). I suspect this has had a negative effect on the Laysan teal's terrestrial prey base as well. Laysan teal observed by Warner (1963) primarily fed terrestrially on cutworm larvae of noctuid moths (*A. dislocata*). Warner considered the brine flies (*N. sexnotata*) to be an incidental part of the diet and described their brine fly chasing behavior as infrequent. Data that are more recent indicate that brine flies are an important component of their diet, at least seasonally (Caspers 1981, Moulton and Weller 1984; this study). Warner (1963) reported a lack of fresh water during his study (conducted in the summers 1957-1961), so it is possible that brine fly abundance was low during Warner's study or that drought conditions prevailed. It is also possible that the terrestrial arthropod community was healthier than it is today, in the wake of an increase of non-native predatory insects introduced to Laysan. Warner hypothesized a shift in diet (more reliance on brine flies) was due to the introduction of a parasitic hymenoptera that feeds on moth larvae, but no research has been carried out on the issue (Kear 1977). Since then, additional predatory hymenoptera (ants) have invaded and are expected to negatively impact native terrestrial arthropods (Reimer 1993, Conant and Roland 1994).

FORAGING EFFICIENCY

Nutrient requirements and foraging efficiency also affect food choices of waterfowl (Krapu and Reinecke 1992). Testing predictions about food choice require that potential prey be ranked by profitability which includes quantity, quality, and search, capture and handling times of prey (Krapu and Reinecke 1992). I did not collect data on capture and handling times, but the prey base on Laysan is relatively simple allowing us to index prey abundance within habitat zones. At the lake, Laysan teal's preference of brine flies over *Artemia* is independent of *Artemia* densities. Food choice was likely related to lower profitability of *Artemia* verses brine flies, but not to the abundance of *Artemia*. When brine flies drop below a profitability threshold (1000 flies per monthly sampling mean; Figure 23), 'other' food is consumed, including larvae of *S. sexnotata* and *Artemia*.

In the terrestrial habitat, some of the most abundant arthropods were selected. Other prey were consumed in lower proportions, perhaps because little time is wasted when a filter feeding duck eats low quality food while simultaneously searching for prey that is more profitable. Ants were present in 45% of the soil samples and occurred in 45%

of fecal samples as well. The actual number of ants counted within each fecal sample was low. This suggests that consumption of ants was incidental to searching for more profitable prey (i.e. lepidopteran larvae and coleoptera), and that ants were not consumed in proportion to their abundance.

Efficient foragers are expected to spend the most time foraging in food patches that are the most profitable (Alonso et al. 1995). Data from behavioral observations and radio telemetry indicate that Laysan teal do indeed spend more time 1) foraging in the terrestrial vegetation types with the greatest abundance of "preferred" prey, 2) spend more time foraging on brine flies (seasonally) when they are most abundant, 3) spend more time in camp during the peak of adult lepidopteran abundance (seasonally) and 4) select the higher quality prey (brine flies) when both brine flies and *Artemia* are at high densities.

The ability of Laysan teal to switch prey under conditions of changing prey abundance was evident from focal scans at the lake. Fecal and invertebrate samples also suggest that the most abundant prey was often the most frequently consumed. However, some abundant invertebrates were not consumed in relation to their abundance. These abundant invertebrates may lack required nutrients or be energetically expensive to process due to high sodium content, for example *Artemia* (Table 13). Other prey not selected may be unpalatable (e.g., ants due to formic acid), difficult to capture, or have defenses against predators (e.g. spiders and cockroaches) rendering them less available as prey.

PREY ABUNDANCE AND REPRODUCTION

The role of food availability in population dynamics of dabbling ducks is not well understood (Owen and Black 1990), yet Cox et al. (1998) showed that the number of invertebrates in brood-rearing wetlands was a good predictor of mallard duckling growth and brood survival. Food abundance affects the female's body condition and her ability to lay and incubate, as well as egg quality, duckling growth and survival (Hunter and Witham 1984, Pelayo and Clark 2002b).

There is evidence to suggest that during poor food years (such as the drought years), reproductive failure on Laysan is likely. Drought and reproductive failure occurred during ENSO events of 1987, 1993, and 1998 (Marshall 1989, Chapter 3). Low brine fly abundance was documented in 1987 and 1998 (Marshall 1989) and reported anecdotally by USFWS field staff in 1993. During the wet La Niña years 1999-2000, higher prey abundance and successful reproduction occurred (see Chapter 3). Brine flies are more sensitive than brine shrimp to higher salinities (Dana and Lenz 1986), which are typical of drought conditions. In other hypersaline ecosystems, high salinities resulted in fewer brine flies (Patten *et al.* 1987, Rubega and Inouye 1994). In drought years when brine fly abundance was low, reproductive failure occurred despite abundant *Artemia*. Drought conditions on Laysan also affect terrestrial invertebrates and plant foods. Abundance of lepidopteran larvae, adult moths, and other arthropods was lower in the drought period monitored in 1998 and represent a decrease in available terrestrial prey. Rainfall on Laysan, through and its effect on food and water availability for Laysan teal appears to have strong influences on their population dynamics (see Chapter 3).

HABITAT USE

The activity pattern of the Laysan teal was characterized by concealment and loafing during the day, primarily in the terrestrial zone. The birds increased their movements between zones in the evening, with more foraging at the lake. Birds were active at night with intensive foraging at both the lake and in the terrestrial zones. This pattern of nocturnal activity and diurnal terrestrial habitat use occurs in some of New Zealand's dabbling ducks (*Anas chlorotis; A. aucklandia*) and may be a strategy of avian predator avoidance. Although frigate birds, and infrequent vagrants (peregrine falcons, short eared owls) are the only avian predators on Laysan, the main Hawaiian Islands had a diverse complement of diurnal avian predators prior to Polynesian colonization (Olson and James 1991). Alternatively, nocturnal foraging may be a response to prey availability, or a means of behavioral thermoregulation in an arid and windy environment.

The coastal zone was not an important foraging habitat of the Laysan teal, unlike New Zealand's *A. chlorotis* and *aucklandia* that frequently feed in coastal habitats (Weller 1980, Williams 1996). Invertebrates associated with wrack and sea kelp are considered important elements of their diet. Laysan's coast typically lacks sea kelp or other high biomass algae, but I suspect the birds would forage on the coast opportunistically, if prey resources were available (e.g. when marine mammal or sea turtle carcasses wash ashore and attracting high densities of arthropods).

DIET

Previous researchers described the Laysan teal as a 100% macro-insectivore (Warner 1963, Moulton and Weller 1984, Moulton and Marshall 1996), however fecal analysis and behavioral observations reveal that seeds and other plant parts are important components of their diet. Most of the granivory and herbivory occurred in the terrestrial zone and therefore, was more difficult to observe than foraging at the lake. The prevalence of terrestrial foraging and the importance of lepidopteran larvae in the diet was first described by Warner (1963). He also described the cutworm larvae climbing the vegetation at night. I did not observe this phenomenon, but found that lepidopteran larvae were common in the soil substrate, particularly in the viney *Ipomoea-Sicyos* vegetation complex. Indeed, this habitat was used more for nocturnal foraging than would be expected by chance.

CONCLUSION

Behavioral flexibility is believed to provide survival advantages for animals (Sol et al. 2002). The Laysan teal consumes a wide variety of prey using a broad foraging strategy. The plasticity exhibited by this species in foraging tactics, substrate use, diet, and breeding improves the chance for successful re-establishment in mammalian predator-free habitats on additional islands. The high risks of extinction for this isolated population, together with the evidence of the species previously wide distribution in Hawaii (Cooper et al. 1996), provide justification for translocation to promote the species' conservation. Although most islands of the Hawaiian archipelago are dissimilar to Laysan, the Laysan teal showed flexibility in their foraging behavior, thus improving the possibilities for successful translocation. The importance of a varied prey base, vegetative cover, a source of fresh water during brood rearing, and the absence of mammalian predators should be emphasized when choosing suitable habitat for new populations.

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Table 1. Vegetation categories and habitat zones of plant species sampled for terrestrial invertebrates.

Category	Habitat Zone	Plant species
Grassy	Terrestrial	*Eragrostis variabilis,* *Fimbristylis cymosa,* *Boerhavia repens*
Viney	Terrestrial	*Ipomoea pes-caprae,* *Sicyos* spp., *Tribulus cistoides*
Shrubby	Terrestrial	*Scaevola sericea,* *Tournefortia argentea*
Matted	Lake	*Sesuvium portulacastrum*, *Heliotropium curassavicum,*
Wetland sedge	Lake	*Cyperus laevigatus*
Mixed	Terrestrial or lake transition	species listed above plus *Portulaca lutea,* *Conyza bonariensis*

Table 2. Examples of behaviors included in activity categories for time activity budgets.

Active	Alert	Foraging	Loaf	Under cover
Self-maintenance: bathe, preen, defecate, stretch	Flush Freeze Look-sky	Search Drink Dabble	Rest Sleep Lying	Subject concealed in vegetation
Social	Vigilant	Snap		
Antagonistic		Probe		
Courtship		Pick		
Mating		Head-dip		
Standing		Up-end		
Locomotion: walk, swim, fly		Fly chasing Nibble vegetation		
Vocalize		Foam-forage		
Other		Swim-snap		

Table 3. Summary of focal observations of Laysan teal collected on Laysan during 1998-2000.

ZONE	DAWN 0400-830 h	DAY 0900-1530 h	DUSK 1600-2030 h	NIGHT 2100-0300 h	ZONE TOTALS
CAMP					
N	22	31	16	0	69
Males	10	12	3	0	25
Females	8	15	11	0	34
Unknown sex	0	0	1	0	1
Radio-tagged males	1	1	0	0	2
Radio-tagged females	2	4	1	0	7
COAST					
N	1	5	32	0	38
Males	0	1	11	0	12
Females	0	4	17	0	21
Unknown sex	0	0	2	0	2
Radio-tagged males	1	0	2	0	3
Radio-tagged females	0	0	0	0	0
LAKE					
N	43	26	81	53	203
Males	4	2	16	18	40
Females	32	19	51	24	126
Unknown sex	4	3	3	9	19
Radio-tagged males	2	0	1	2	5
Radio-tagged females	1	4	10	3	18
TERRESTRIAL					
N	12	39	25	16	92
Males	4	12	9	7	32
Females	8	13	14	9	44
Unknown	0	0	1	0	1
Radio-tagged males	2	4	0	0	6
Radio-tagged females	1	10	1	3	15
SESSION TOTALS	27	78	50	35	190

Table 4. Estimates of habitat available on Laysan Island in hectares.

Habitat zone	Area available	Vegetation type	Area available
Camp	3	Bunch grass	113
Coast	118	Viney vegetation	41
Lake	104	Mixed vegetation	51
Terrestrial	190		
Island	415		

Table 5. Summary of activity budget of the Laysan teal by session and ANOVA results.

Activity	Morning	Day	Evening	Night	ANOVA	p
Active	0.39	0.15	0.26	0.28	F=1.29	0.279
Alert	0.05	0.04	0.11	0.04	F=1.82	0.144
Forage	0.16^{AB}	0.04^{A}	0.22^{B}	0.46^{C}	F=18.50	<0.0001
Loaf	0.18	0.20	0.31^{A}	0.11^{B}	F=4.33	0.005
Under cover	0.21	0.56^{A}	0.10	0.10	F=23.84	<0.0001

Tukey's pairwise comparisons of behaviors by time session indicate differences between groups lettered with different superscript A, B, or C.

Table 6. Frequency of occurrence (percent of samples with prey types) of taxa in Laysan teal fecal samples collected on Laysan Island during 1985 and 1998-2000.

Year	N	Prey type	Percent of samples analyzed
1998-2000[1]	118	Diptera adult	47
		Dipteran larvae/pupae	39
		Formicidae	36
		Seeds	31
		Lepidopteran larvae	25
		Coleoptera	23
		Plant fibers	17
		Artemia	15
		Acari	11
		Amphipoda	8
		Unknown arthropod	7
		Blattaria	3
		Diptera terrestrial	3
		Lepidopteran adult	3
		Araneida	2
		Dermoptera	0
1985[2]	28	Diptera adult (*Scatella sexnotata*)	39
		Artemia	32
		Lepidopteran larvae	32
		Blattaria	21
		Dipteran larvae (*Scatella sexnotata*)	21
		Amphipoda	14
		Dipteran terrestrial	11
		Acari	7
		Araneida	7
		Formicidae	4
		Dermaptera	4
		Coleoptera	0
		Lepidopteran adult	0
		Plant fibers	0
		Seeds	0

[1] MHR data from samples collected from all habitats and seasons.

[2] (Lenz and Gagne 1986) unpublished data from samples collected from the lake zone in 1985.

Table 7. Number of prey items and percent of total items identified in Laysan teal fecal samples collected on Laysan Island 1998-2000 (N=62 samples).

Prey type	Number	Percent of total items
Dipteran adult	725	31.9
Artemia	472	20.7
Dipteran larvae or pupae	355	15.6
Lepidopteran larvae	188	8.3
Total Seeds	179	7.9
Portulaca seeds	85	(47.4 % of seeds; 3.7 % of total items)
Plant fiber	149	6.6
Coleoptera	81	3.6
Formicidae	47	2.0
Amphipoda	37	1.6
Lepidopteran adult	13	0.5
Acari	12	0.5
Dipteran terrestrial	9	0.3
Blattaria	3	0.1

Table 8. Results of Kruskal Wallis tests compares taxa counting in fecal samples from lake and terrestrial zones.

Taxa counted	H	P-value
Amphipods	0.77	0.38
Ants	6.43	*0.01
Artemia	2.44	0.12
Coleoptera	1.84	0.18
Diptera adult	4.25	*0.04
Diptera larvae or pupae	1.08	0.3
Lepidoptera larvae	7.61	>*0.001
Plant fiber		
Seeds	5.52	*0.02

*Significant at 95% level

Table 9. Observation of food items and water consumed during focal observations.

Consumption observed	Camp	Coast	Lake	Terrestrial	Total Observation
Algae			11		11
Amphipod			1		1
Artemia			2		2
Brine fly			1274		1274
Blattaria				5	5
Terrestrial diptera	49		155	481	685
Maggot			6	99	105
Moth	37				37
Portulaca	4			2	6
Seeds				36	36
Spider	1				1
Unk. soil inverts.				20	20
Unknown	11	1	15	33	60
Water	181	27	220	31	459

Table 10. Invertebrate prey diversity from foraging substrates; grass, vine, and mixed vegetation associations. Substrates were sampled between 1998-2000.

Vegetation type	Grass		Vines		Mixed	
Substrate	soil N=302	standing vegetation N=231	soil N=101	st. veg. N=67	soil N=84	st. veg. N=69
Simpson's Reciprocal (N_2)	5.26	4.79	6.19	1.93	7.57	5.50
Shannon-Weiner Function H'	2.80	2.73	2.97	1.41	3.18	2.78
No. of equally common taxa	6.96	6.66	7.83	2.66	9.06	6.87
Total taxa = 16	15	14	16	12	14	13

Table 11. Laysan Island's daily rainfall means (mm) and standard deviations.

Month	1998	1999	2000
January	0.78 ± 1.78	4.56 ± 8.84	5.11 ± 9.02
February	0.67 ± 1.62	4.53 ± 13.49	1.37 ± 2.85
March	1.52 ± 4.19	2.06 ± 4.34	2.13± 4.17
April	1.54 ± 4.27	1.95 ± 4.22	0.57 ± 1.17
May	0.60 ± 1.00	7.80 ± 14.47	1.21 ± 1.82
Jun	1.85 ± 4.68	1.47 ± 3.28	1.97 ± 6.09
July	4.10 ± 6.28	3.44 ± 8.39	3.04 ± 4.86
August	3.76 ± 8.86	1.34 ± 2.90	1.46 ± 2.39
September	5.33 ± 17.82	1.13 ± 2.05	3.95 ± 12.54
October	1.91 ± 3.32	1.82 ± 3.07	2.20 ± 3.74
November	1.75 ± 4.71	7.51 ± 14.79	6.87 ± 16.66
December	3.67 ± 5.85	3.06 ± 7.64	2.69 ± 5.44
YEARLY TOTAL	1.98 ± 1.75	3.93 ± 2.33	3.30 ± 2.27

Table 12. Indices of preference (w) for select prey types from terrestrial zone based on abundance (all dates combined) from soil and standing vegetation sampling and the number of prey items counted in fecal samples (N=62).

Prey type	Amt. prey[1]	Proportion prey	Prey counted in fecal samples	Proportion prey in fecal samples	95% CI	(w)[2]	Bonferroni 95% CL	Standardized selection index B[3]
Soil samples N=487								
Larval Lepidoptera	366	0.26	188	0.63	0.55-0.70	2.42*	2.00-2.83	0.45
Gastropoda	301	0.21	0	0.0	0-0	0	0	0
Coleoptera	225	0.16	76	0.25	0.18-0.32	1.59*	1.08-2.05	0.29
Amphipoda	150	0.11	34	0.11	0.06-0.16	1.07	0.54-1.59	0.20
Other	136	0.10	0	0.0	0.0	0	0.0	0
Isopods	134	0.10	0	0.0	0.0	0	0.0	0
Arachida	67	0.05	1	0.003	0-0.01	0.07	0-0.26	0.01
Standing Veg. N=367								
Coleoptera	2132	0.40	76	0.77	0.66	1.91*	1.62-2.19*	0.56
Arachnida	1158	0.22	1	0.01	0-0.04	0.05	0-0.17	0.01
Adult Lepidoptera	880	0.17	13	0.13	0.04-0.22	0.79	0.26-1.32	0.23
TZ Diptera[4]	721	0.14	9	0.09	0.02-0.01	0.67	0.12-1.22	0.20
Gastropoda[5]	407	0.08	0	0.00	0-0	0	0	0

[1] Amount prey =invertebrate abundance is the pooled total of abundant taxa identified during sampling from 1998-2000.

[2] *w*= proportion of prey used by Laysan teal/proportion of prey available in the environment (estimated).

[3] B = standardized selection index. Values less than 1 divided by the number of resources indicate no preference and values above or below provide evidence of "preference and avoidance", respectively.

[4] The taxa category "Diptera" from the fecal samples was excluded from the analysis because it included mixed species, some from the wetland habitat. Taxa in fecal samples identified as terrestrial diptera were likely underestimated due to the difficulty in separating and identifying members of this order.

[5] Both live and dead gastropods were included in the total abundance; therefore live prey is likely to be overestimated.

* Indicates strong evidence of selection.

Table 13. Pearson's correlation coefficients with Bonferroni probabilities for habitat use and resource abundance of radio telemetry birds.

Resource	Camp	Coast	Lake	Terrestrial
Artemia *(edge)*[2]	-0.26 p=0.99	-0.09 p=0.99	0.39 p=0.84	-0.19 p=0.99
Artemia *(interior)*[2]	-0.03 p=0.99	-0.03 p=0.99	0.41 p=0.81	-0.47 p=0.66
Brine flies[1]	0.19 p=0.63	-0.40 p=0.99	-0.37 p=0.27	0.31 p=0.68
Coleoptera[4]	0.38 p=0.99	0.48 p=0.96	-0.50 p=0.99	0.19 p=0.99
Lepidoptera (camp)	0.74 p=0.05*	0.40 p=0.97	-0.37 p=0.98	-0.13 p=0.35
Lepidoptera (soil)[3]	0.04 p=0.01	-0.15 p=0.99	0.56 p=0.41	-0.57 p=0.99
Rain[1]	0.01 p=0.98	-0.28 p=0.99	0.28 p=0.99	-0.24 p=0.89
Soil prey[3]	0.34 p=0.98	0.09 p=0.99	0.16 p=0.99	-0.38 p=0.99
Vegetation prey[4]	0.57 p=0.40	0.55 p=0.99	-0.45 p=0.99	-0.01 p=0.99

[1] April-July 1998; November 1998-October 1999; April-July 2000; =16 observations

[2] June/July 1998; November 1998-October 1999; N=12 observations

[3] June/July 1998; November 1998-October 1999; April-July 2000: N=14 observations

[4] November 1998-October 1999; April-July 2000: N=13 observations

* Significant at the 95% level

Figure 1. Laysan teal chasing brine flies on the mudflats of Laysan Island. Birds run through flies, flush swarms, and then snap flies out of the air.

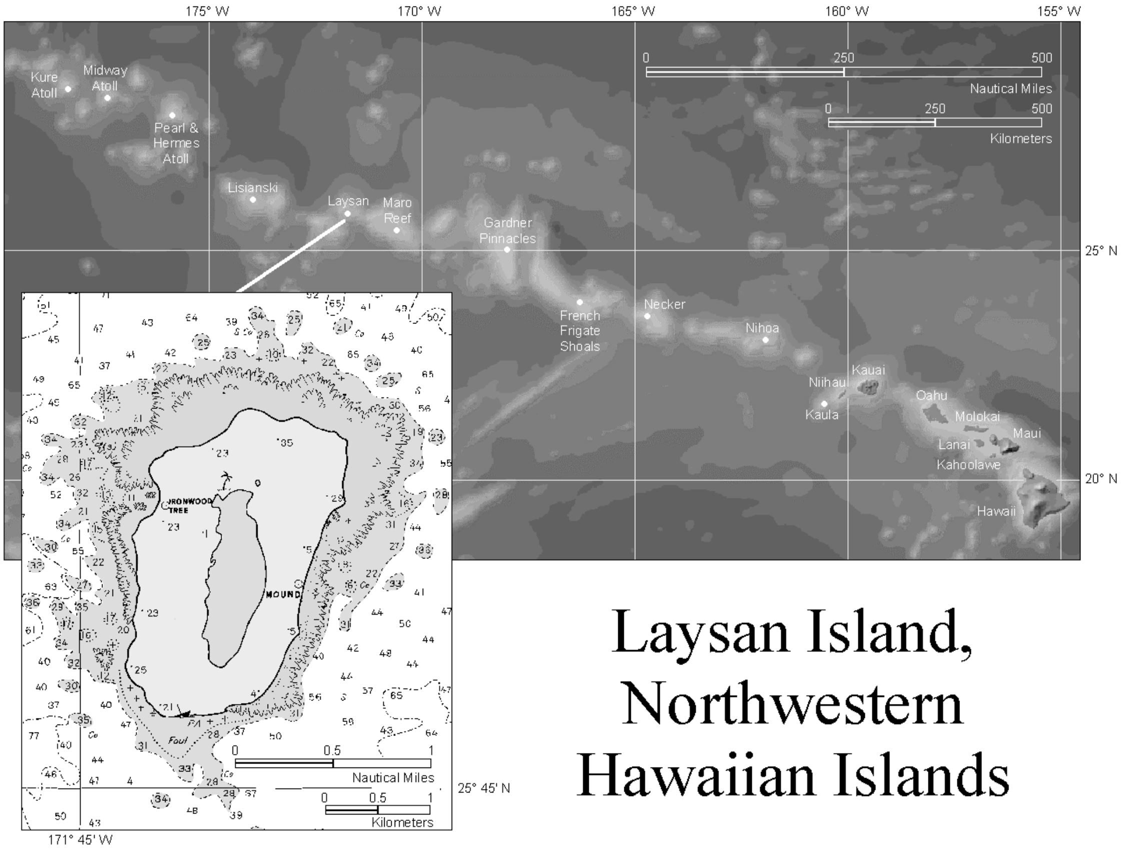


Figure 2. Map of Hawaiian archipelago with detail of Laysan Island.

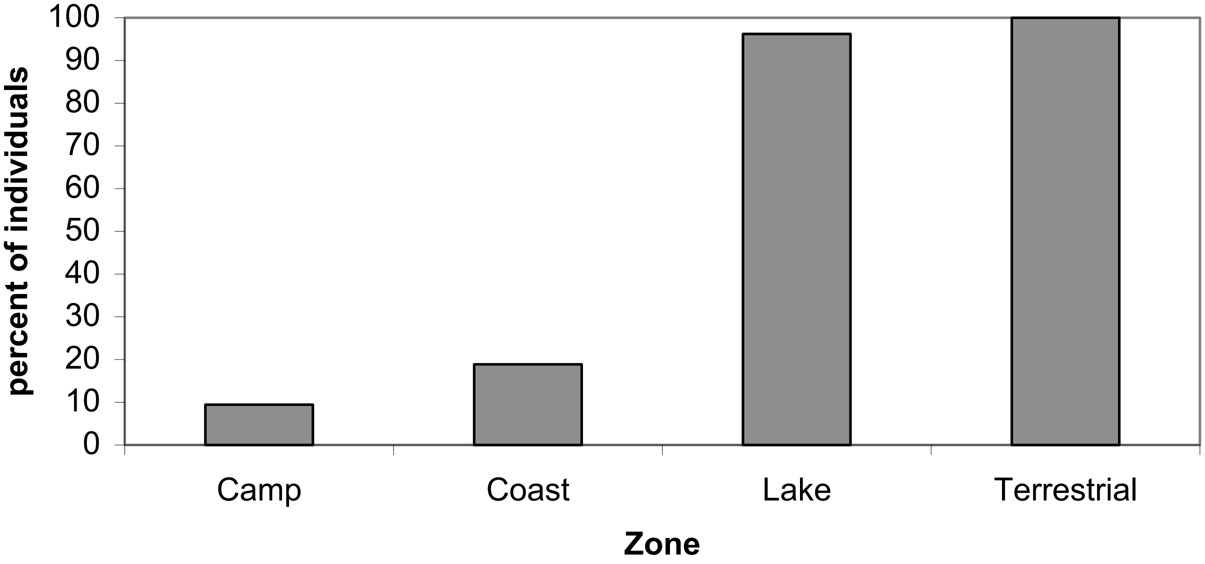


Figure 3. Summary of individual habitat use by radio-tagged Laysan teal on Laysan Island during 1998-2000. Birds included were located 10 or more times (N=53; 1562 locations).

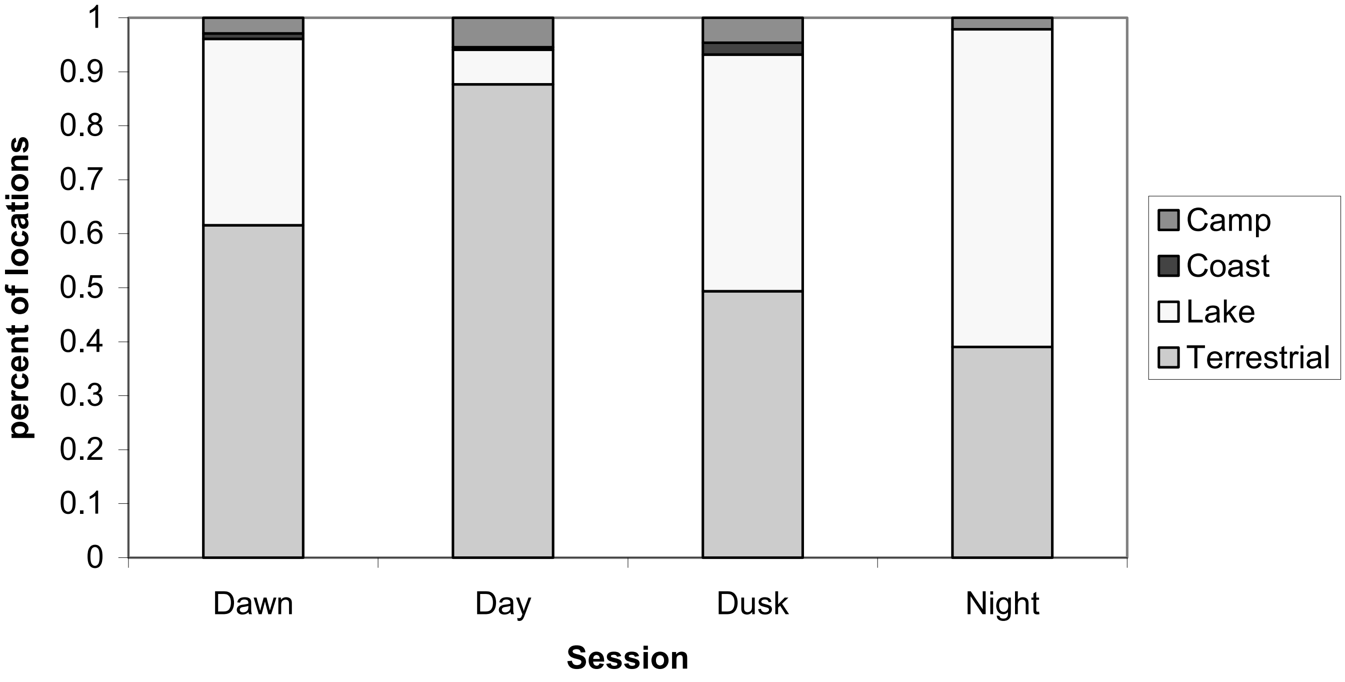


Figure 4. Daily habitat use by radio-tracked Laysan teal 1998-2000 (N=62 birds, 1634 locations)

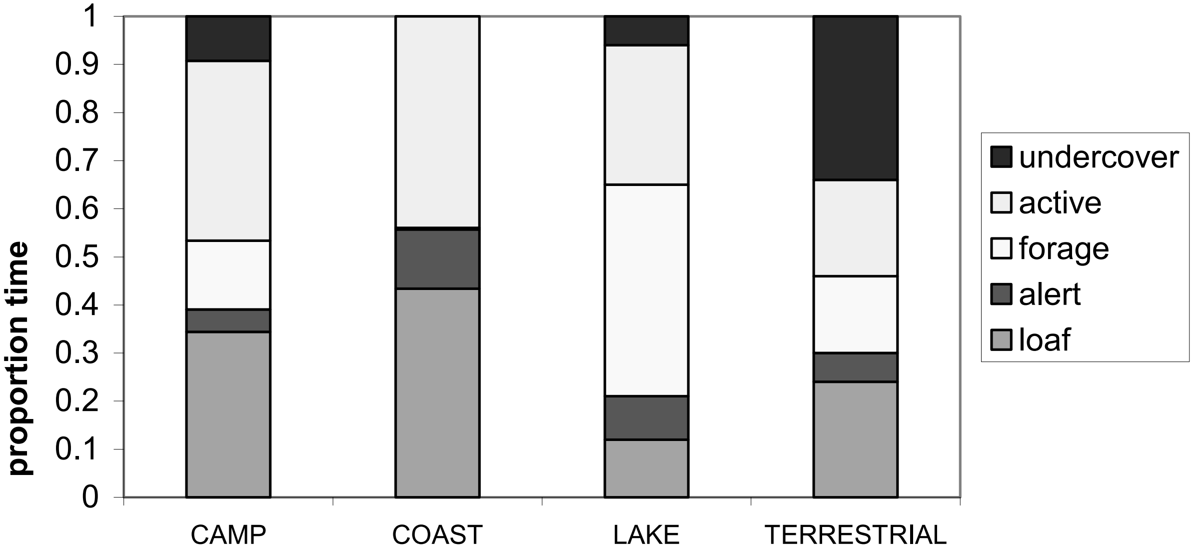
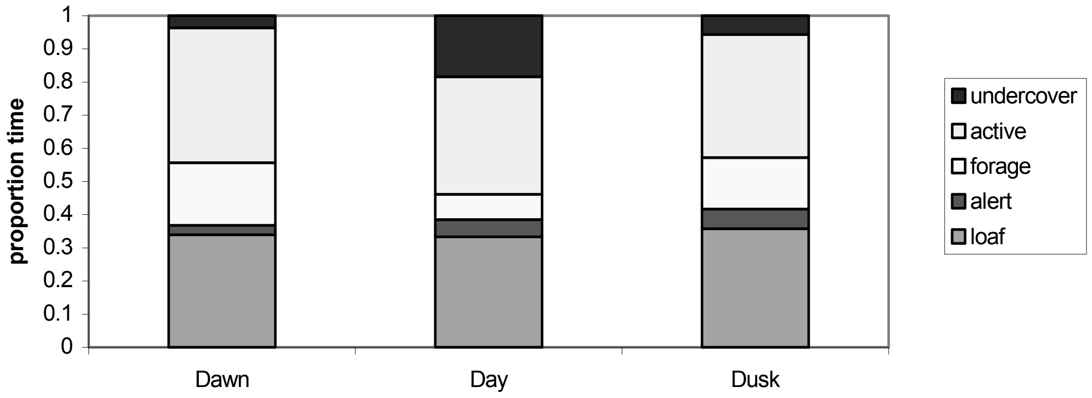
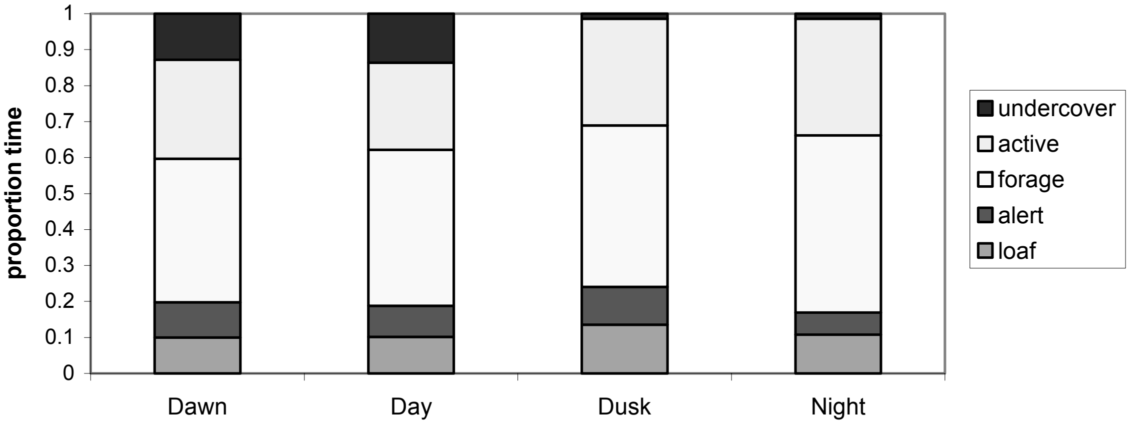


Figure 5. Time activity budget of Laysan teal in habitat zones of Laysan Island (N= 402; 8511 min).



6a. Camp (N= 67 observations)



6b. Lake (N=276 observations)

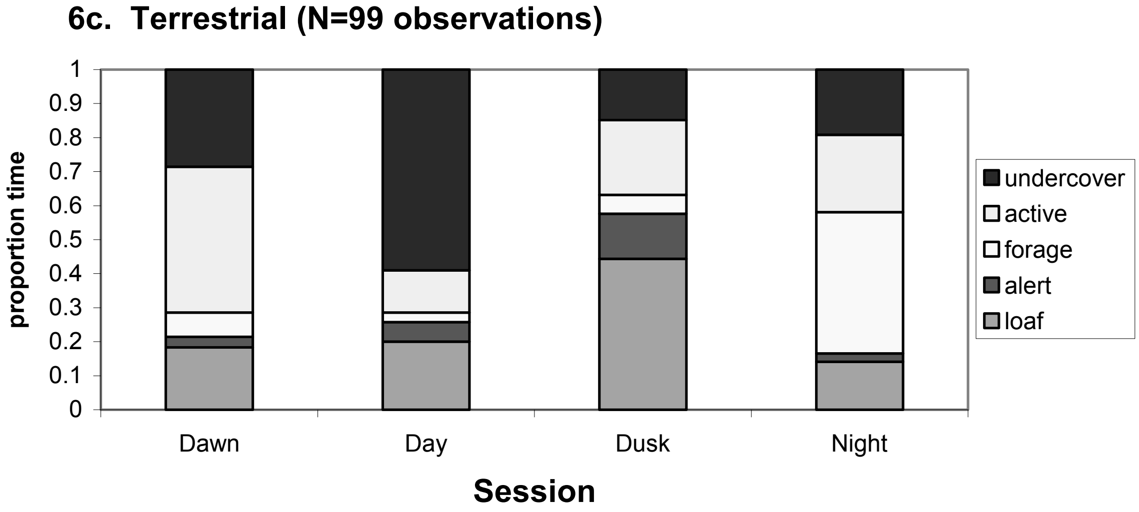


Figure 6. Time activity budget of the Laysan teal by habitat zones and time sessions 1998-2000; a) camp, b) lake, and c) terrestrial zones.

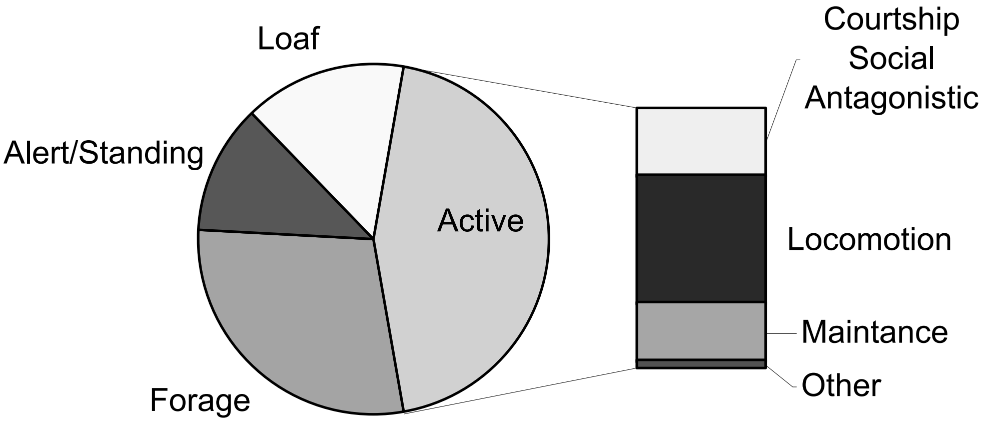


Figure 7. Behavior scans at the lake 1 hr before sunset (N=179 scans).

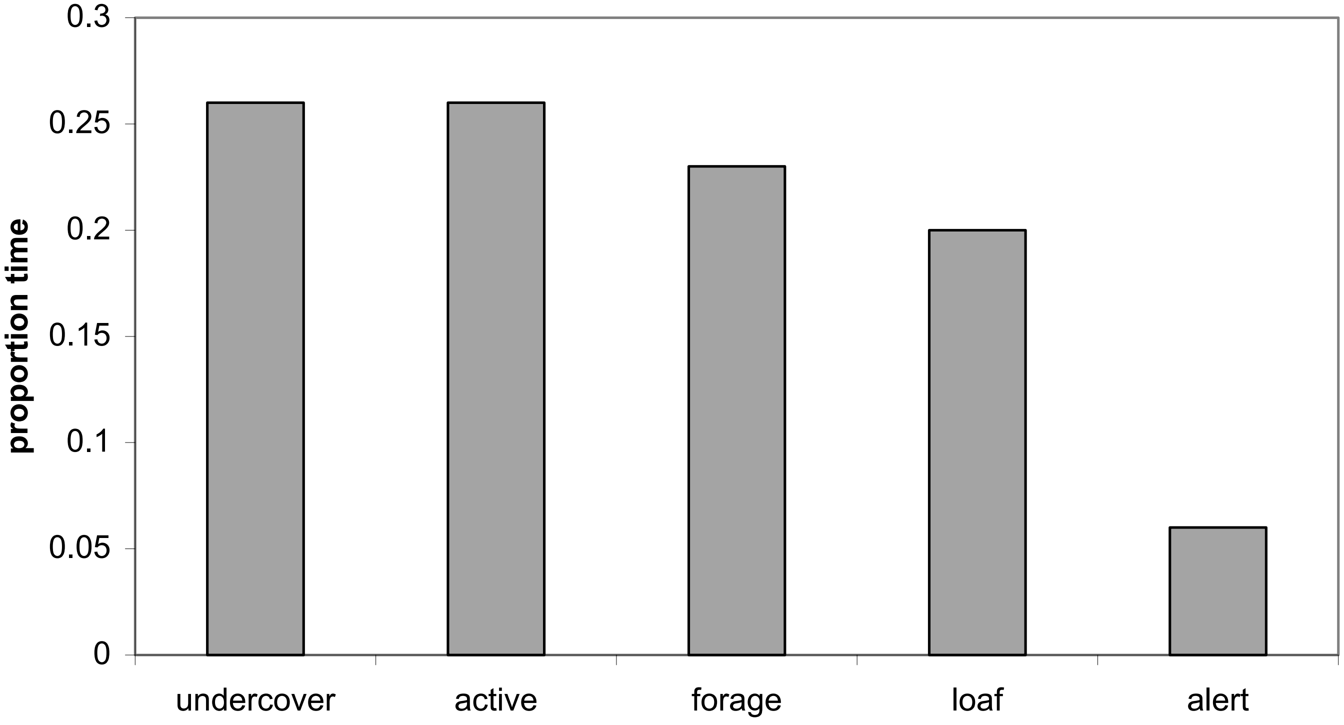
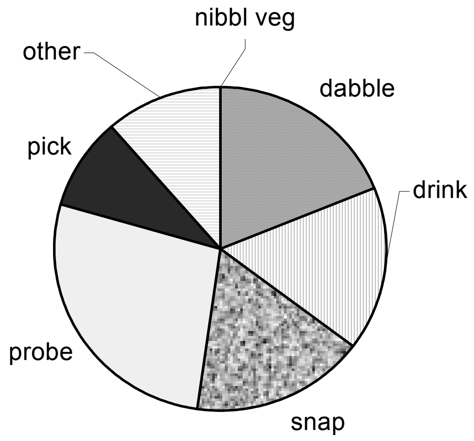
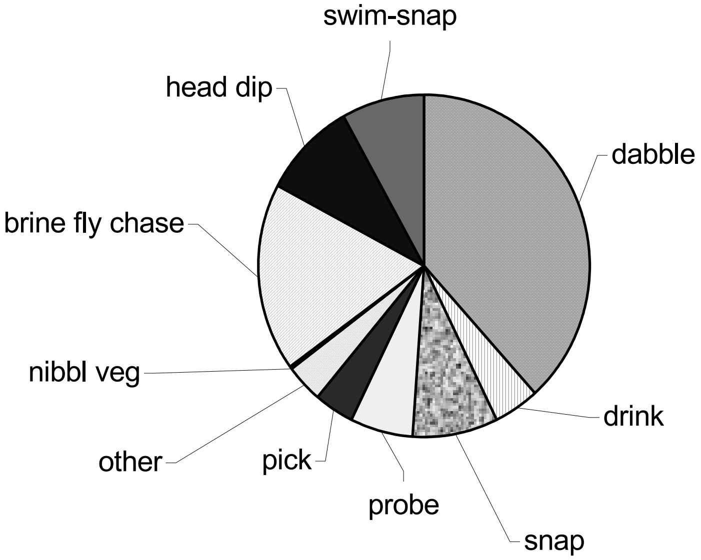


Figure 8. Total time activity budget of the Laysan teal on Laysan Island 1998-2000.



9a. Camp



9b. Lake

9c. Terrestrial

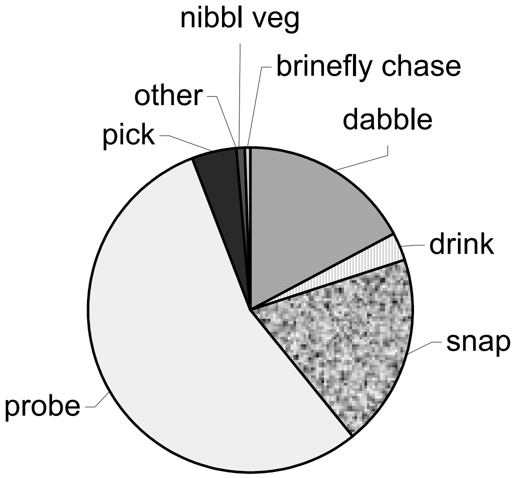
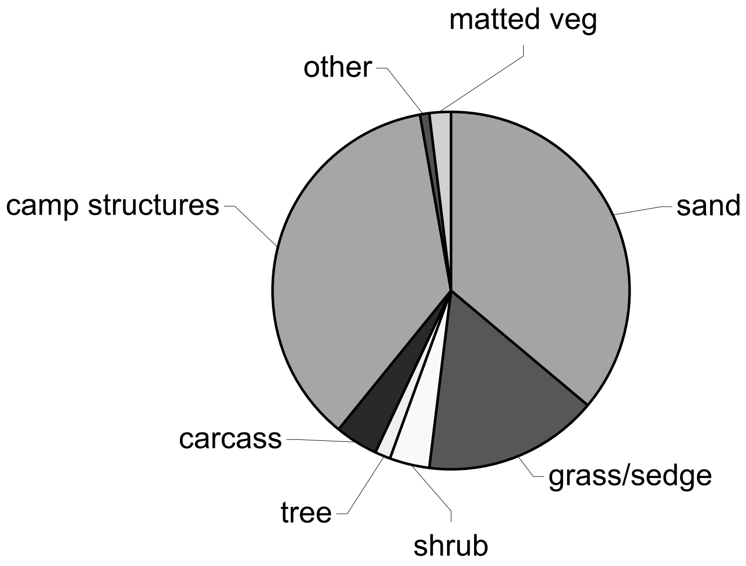
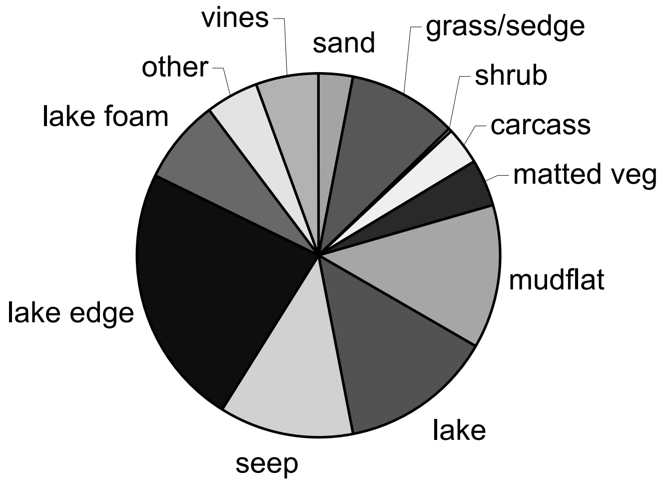


Figure 9. Foraging behavior of the Laysan teal in the habitat zones of Laysan Island: a) camp (N= 67 observations; 1304 min), b) lake (N=276; 4656 min), and c) terrestrial (N=99; 1793).

10a. Camp



10b. Lake



10c. Terrestrial

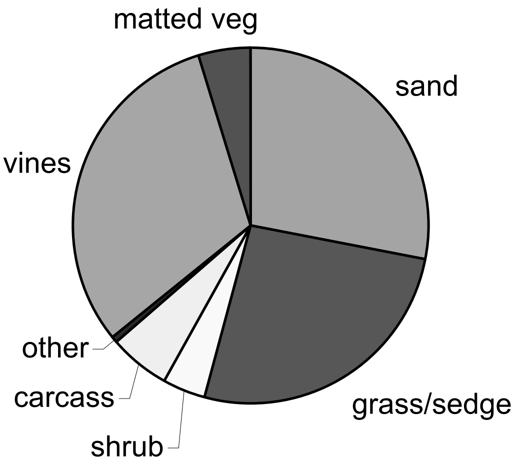


Figure 10. Substrate use of the Laysan teal in the a) camp, b) lake, and c) terrestrial zones 1998-2000 (N=442 focal observations).

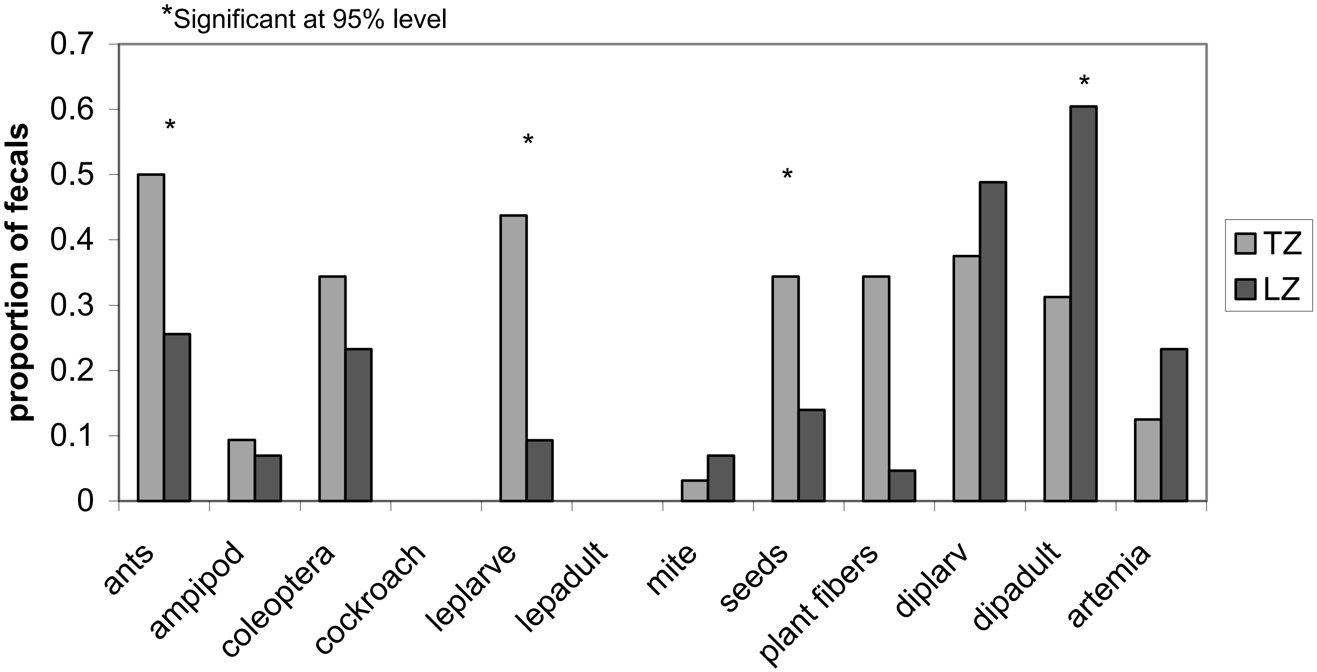


Figure 11. Frequency of prey items in fecal samples collected from lake (N=45) and terrestrial (N=30) zones.

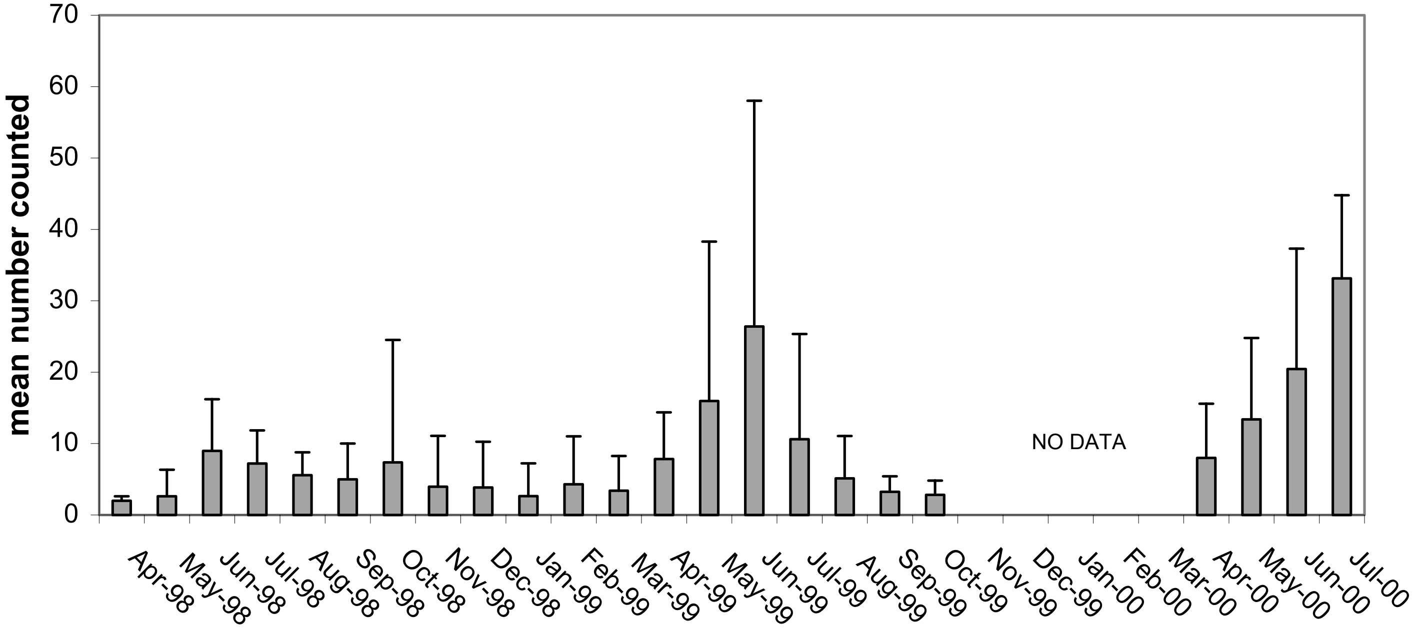


Figure 12. Daily count mean (+SD) of adult lepitopteran in camp tent traps April 1998-July 2000.

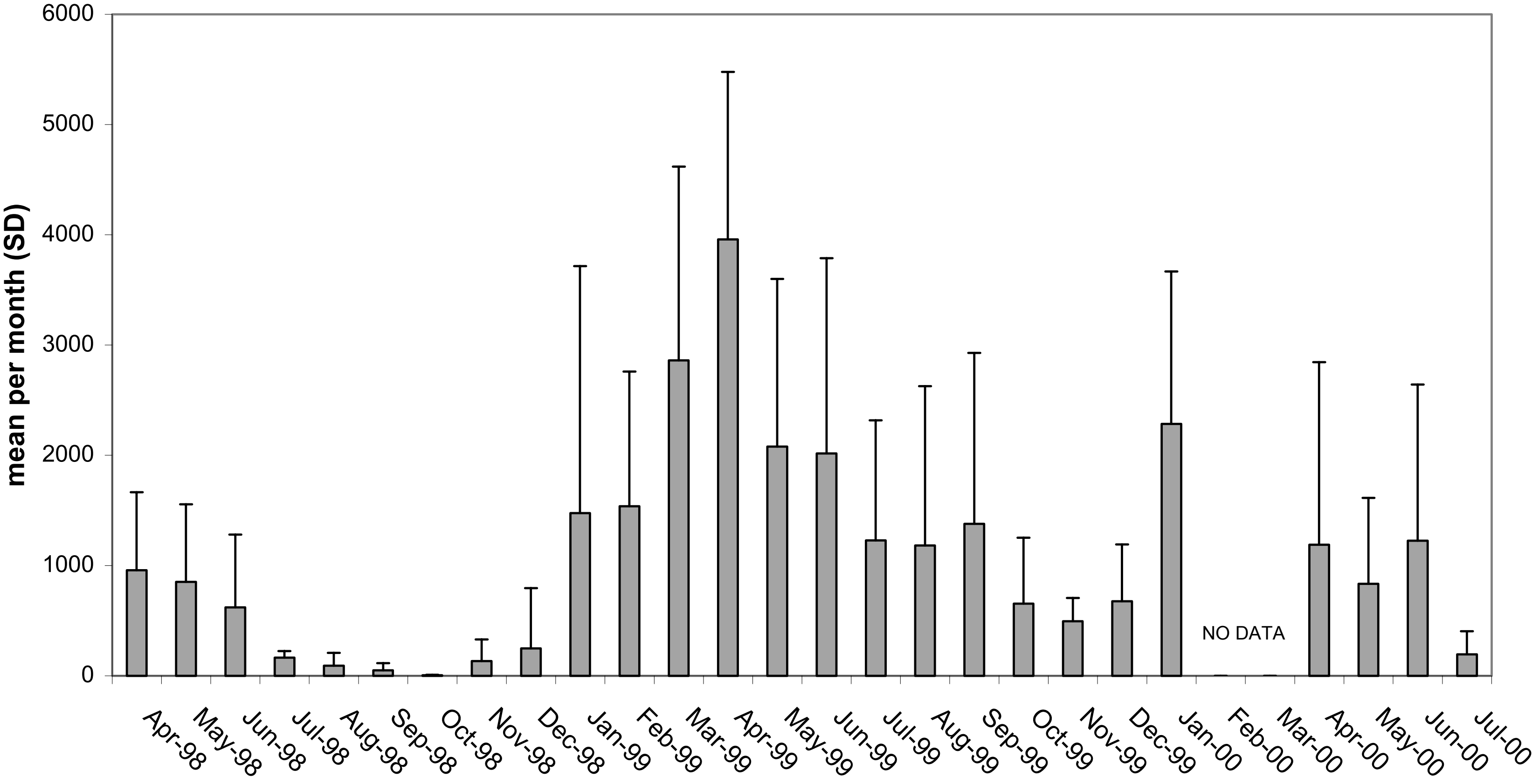


Figure 13. Seasonal brine fly (Ephidridae) abundance: monthly means (+SD) March-February 2000.

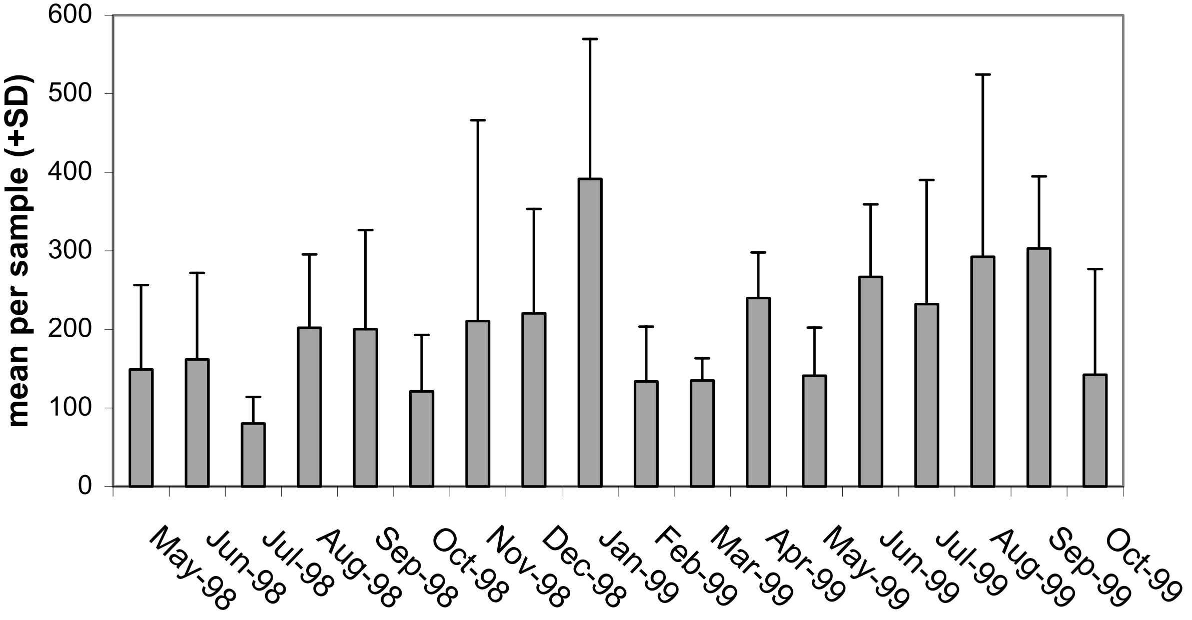


Figure 14. Vertical *Artemia* tows from lake center May 1998-October 1999 (N=270 samples).

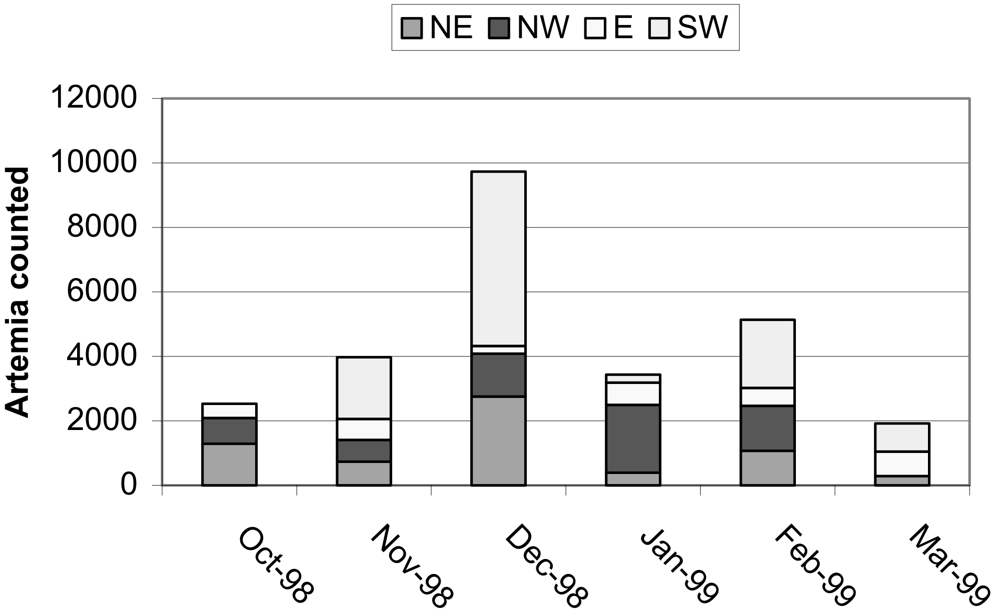


Figure 15. Horizontal *Artemia* tows at four lake edge sites around Laysan's lake (N=30 tows).

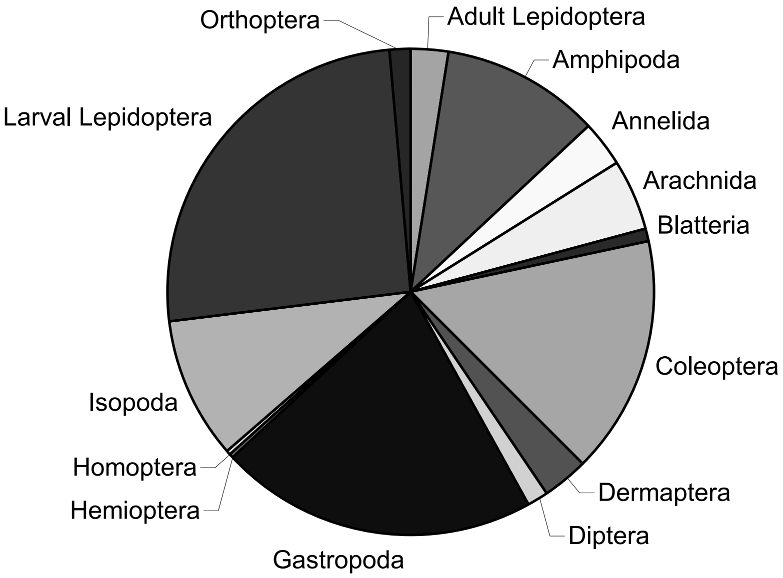


Figure 16. Macro-invertebrate composition of N=487 soil sample sieves collected in terrestrial habitats of Laysan 1998-2000.

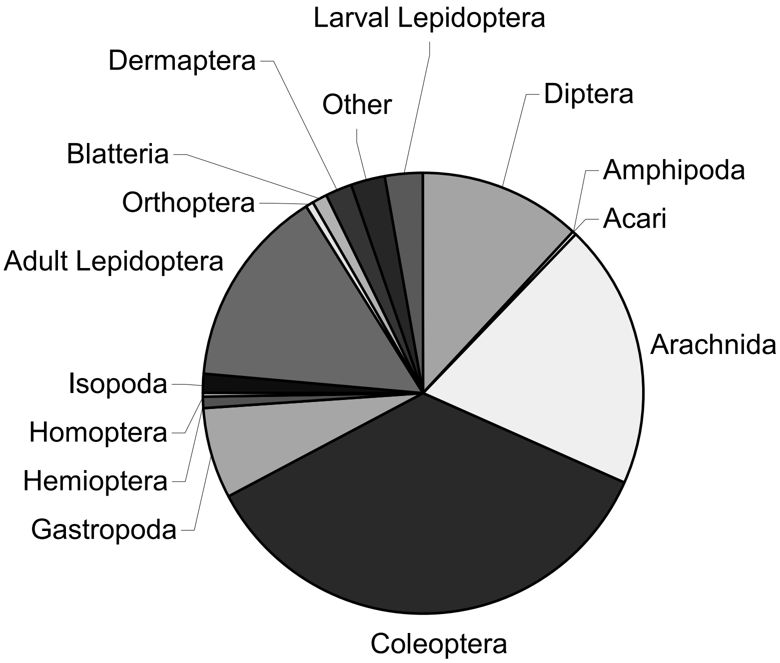


Figure 17. Macro-invertebrate composition of N=367 standing vegetation beat samples collected in terrestrial habitats of Laysan 1998-2000.

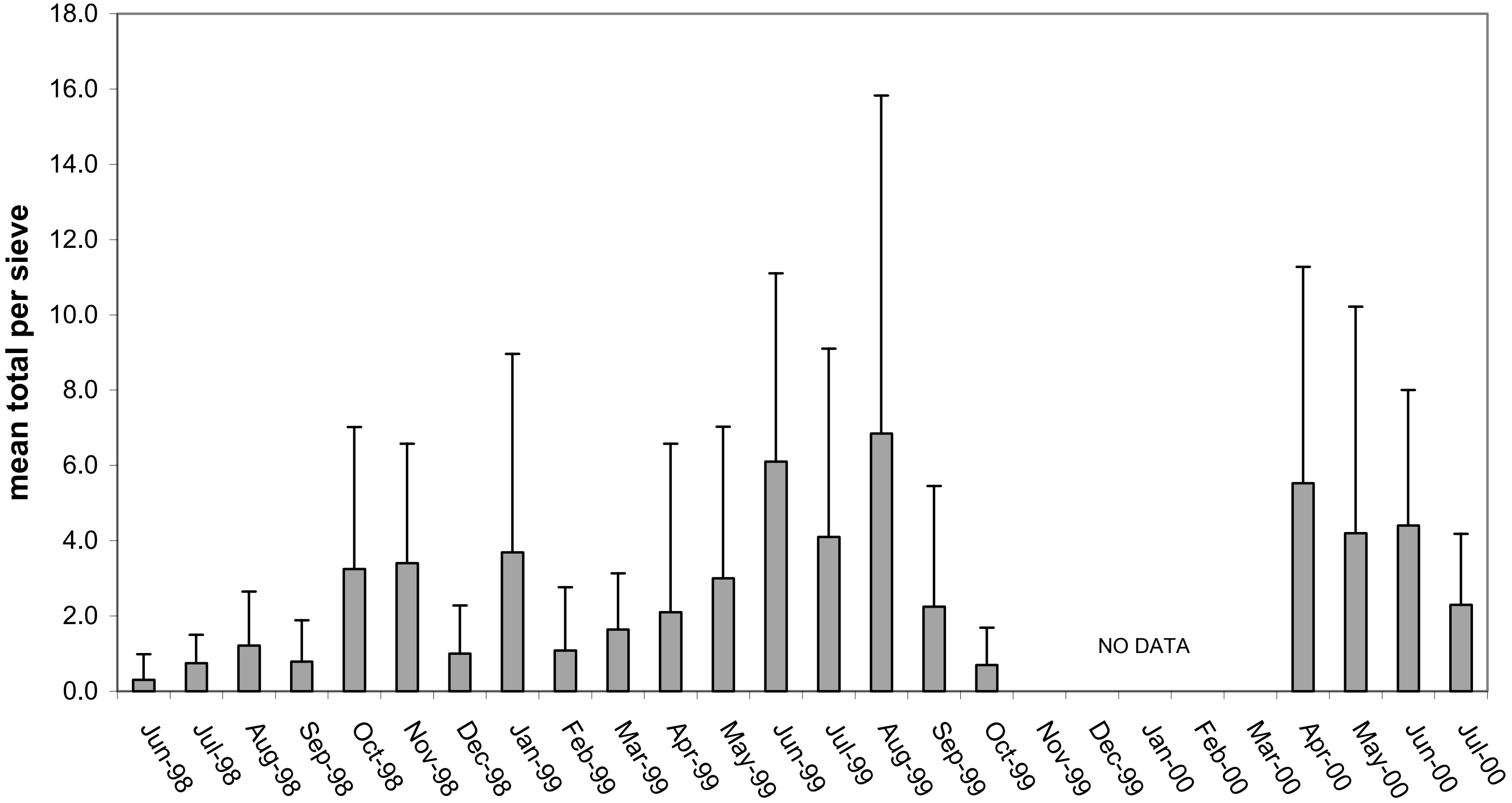


Figure 18. Seasonal prey abundance (mean +SD) from terrestrial habitats: soil sieves collected from June 1998-July 2000 (N=487 samples).

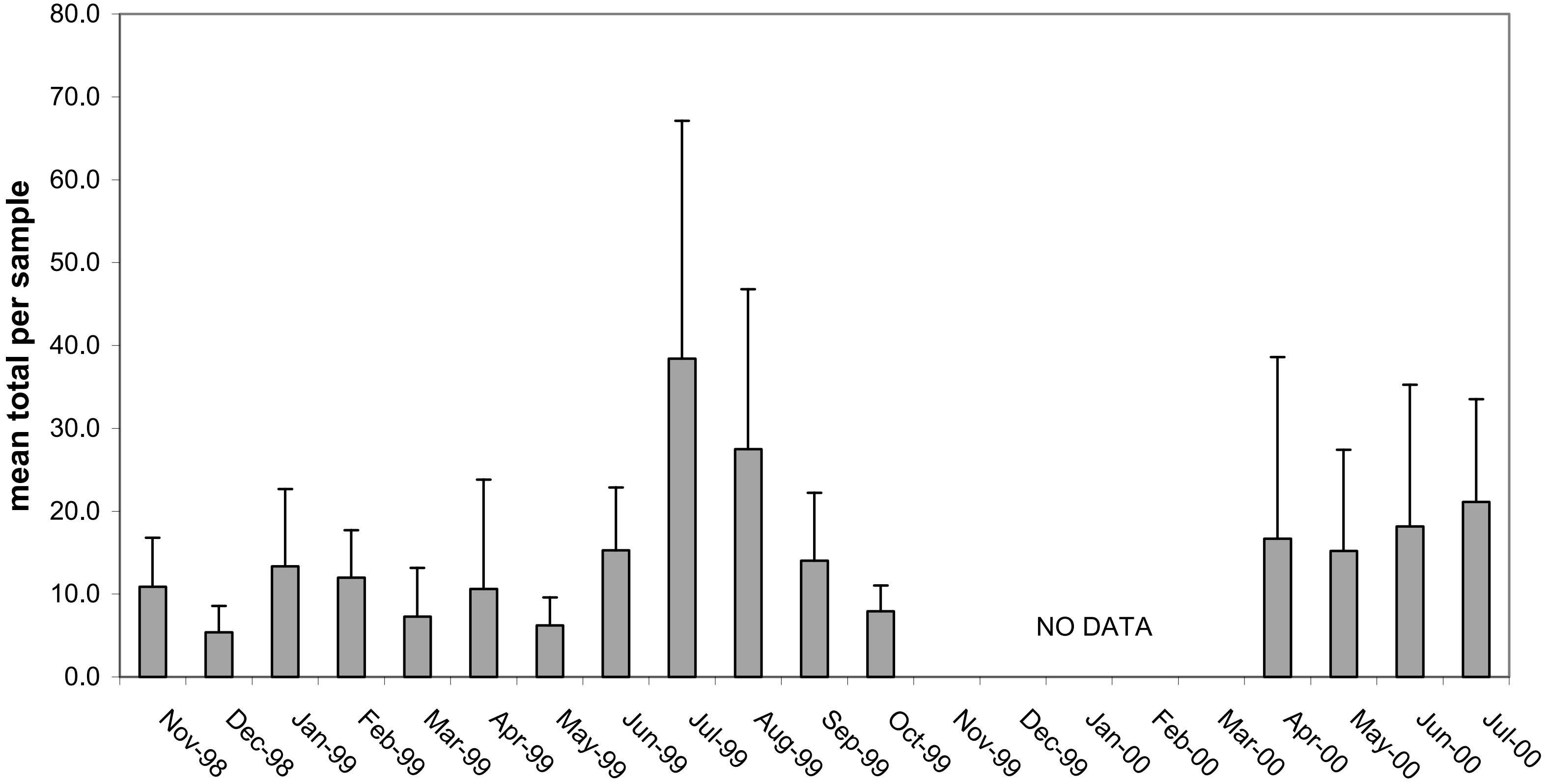


Figure 19. Seasonal prey abundance (mean +SD) from terrestrial habitats: standing vegetation from Nov. 98 - July 2000 (N=367 beat samples).

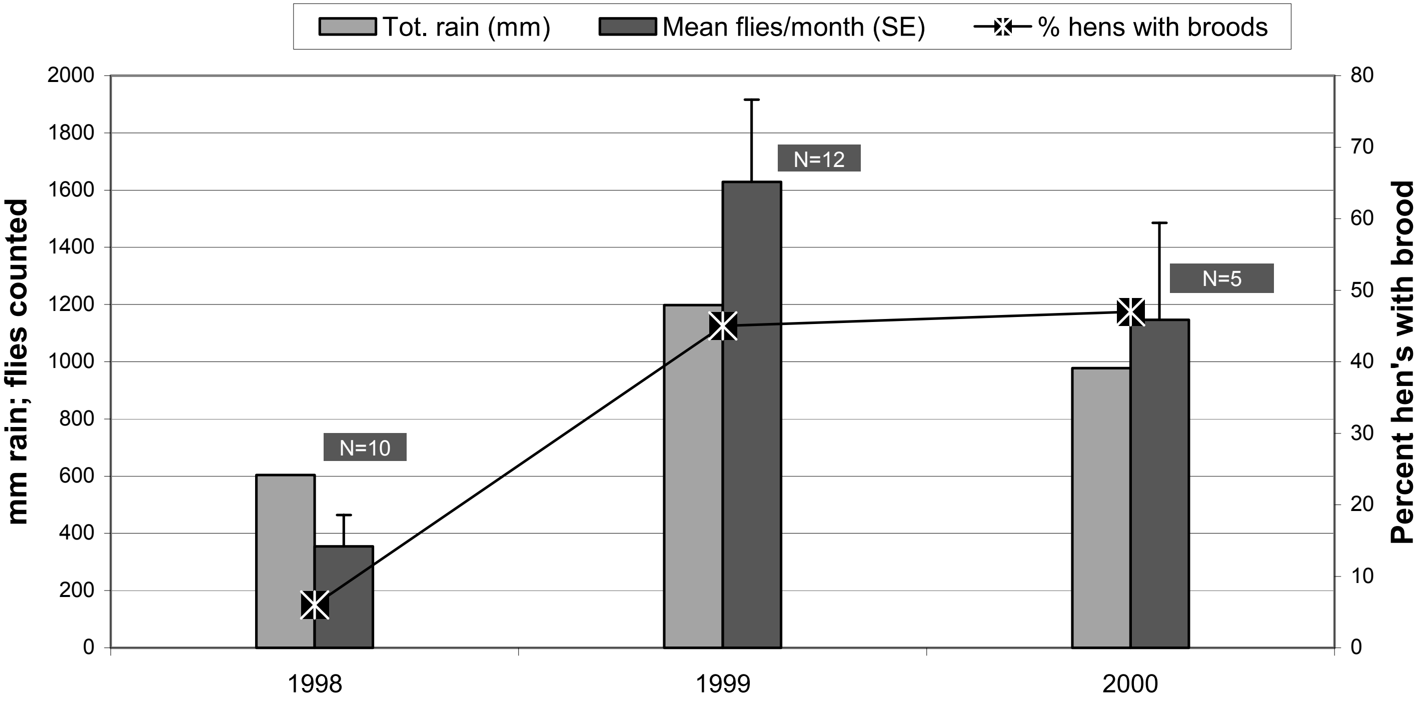
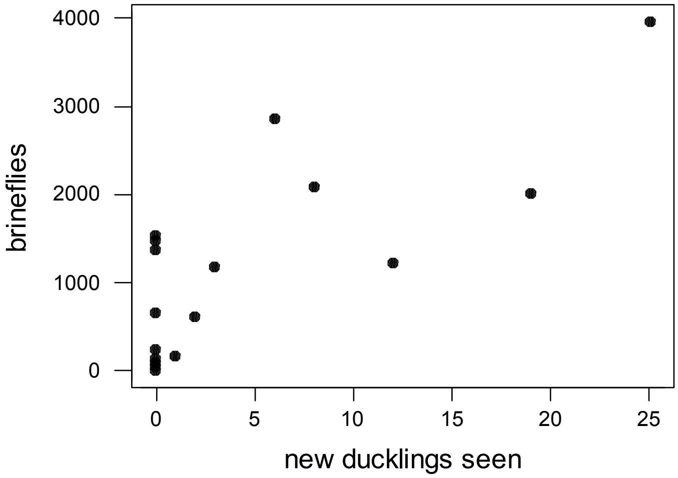


Figure 20. Annual variation in rainfall, mean brineflies (N=months sampled), and breeding success of Laysan teal 1998-2000.



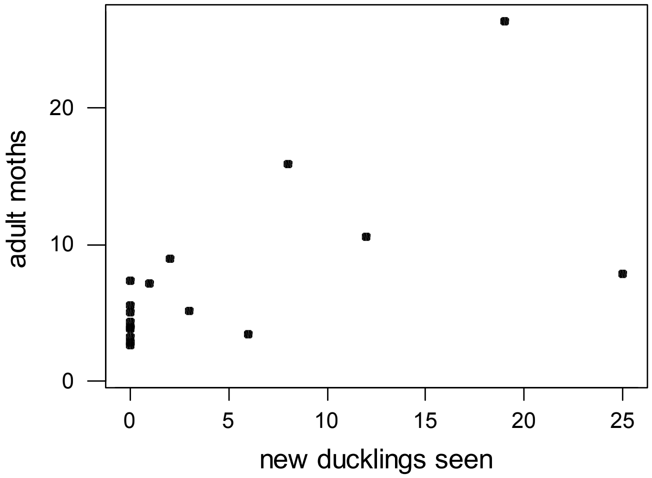


Figure 21. Relationship between monthly brood production and abundance of select prey (monthly mean brine flies and adult moths 1998-1999).

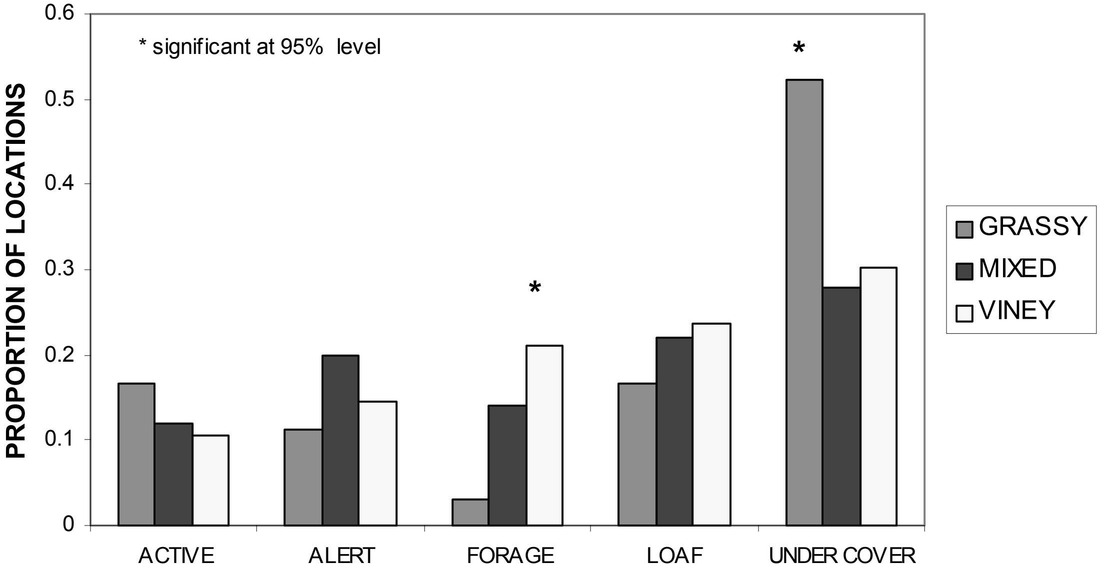


Figure 22. Instaneous activity of visually detected radio tracked birds in the terrestrial zone (N= 58 birds; 258 locations).

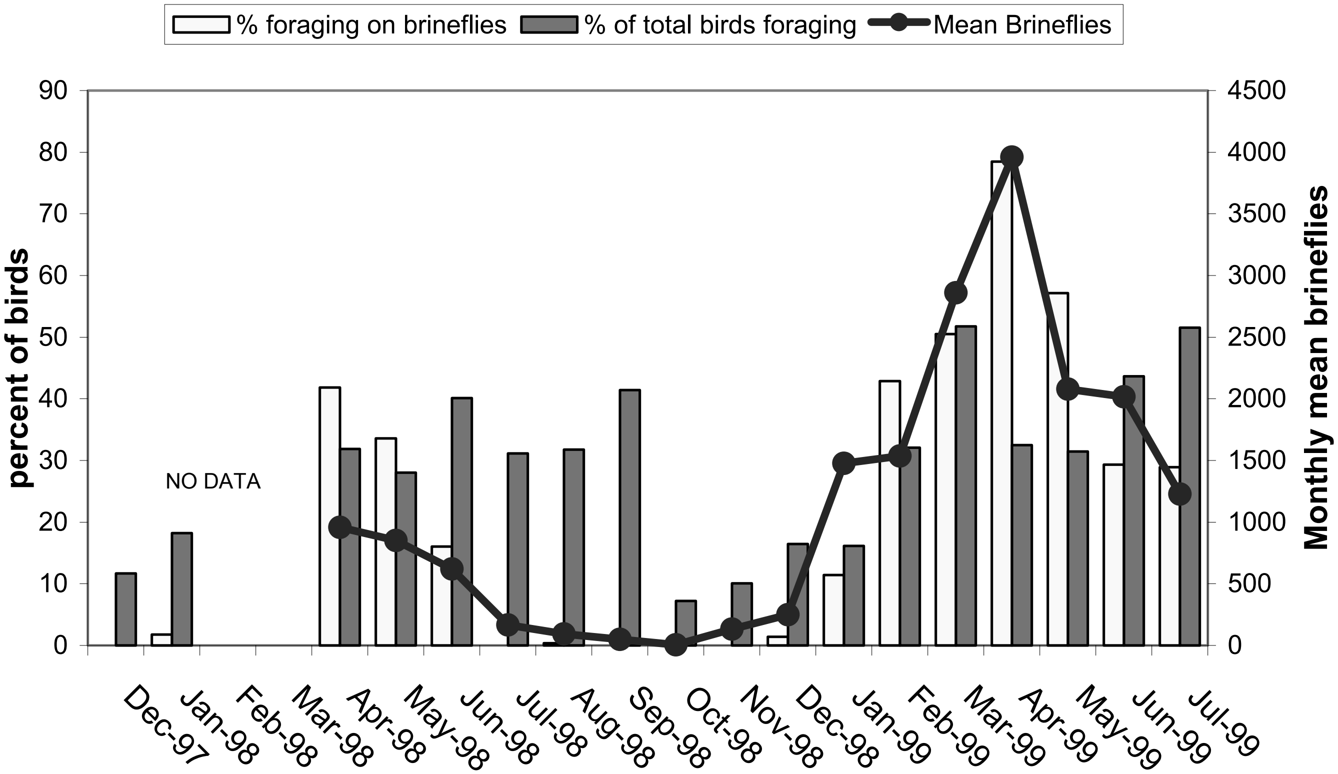


Figure 23. The relationship between the total birds foraging, birds foraging on brine flies and brine fly abundance. Laysan teal behavioral scans were conducted at the lake 1 hr before sunset 1998-1999 (N=179 lake scans; 20,446 obs.).

Appendix 1. Descriptions of Laysan teal behaviors.

Behavior	Description
Antagonistic	Displays or aggression, threats, males may pull each other's breast feathers
Bathe	Stereotyped movements to wet the feathers: fluffing the feathers, rapidly flicking the wings, diving, and dousing feathers. Usually occurs in the ocean or tide pools.
Brood	Hen covering the young to protect, shield, or keep them warm
Courtship	Various displays and ritualized movements used as signals between breeding birds: examples include chin-lifting, wing flapping, head bobbing
Dabble	Filter feeding or sieving food with the bill from water, mud, or dry sand.
Drink	Dipping the bill and tipping the head back to let water run down the throat and be swallowed.
Flush	Fly from vegetation; usually a result of disturbance
Fly chase	Pursues diptera prey on the ground while running
Foam forage	Takes food items encountered in wind generated saltwater foam
Freeze	Alarm stance without movement
Head-dip	Takes food from the water with head submerged
Loaf	Sleep, rest, posture
Look-sky	Bird tilts head laterally and watches the sky
Pick	Selects particular prey items from the substrate; often seeds, and leaves
Preen	Cleaning, rearrangement, and oiling of feathers with bill
Probe	Inserts bill into the substrate and locates prey by touch
Search	Directed locomotion movement interrupted only with foraging tactics
Snap	Taking prey (usually flying insects) by snapping it out of the air
Social	Vocalizations and non-aggressive interactions
Standing	Awake but immobile
Swim-snap	Taking prey (usually flying insects) by snapping it from the air while swimming
Under cover	Concealed in vegetation
Up-end	While floating on the surface in shallow water, birds pivot headfirst downward to reach submerged food on or near substrate.
Vigilant	Alert, upright postures

CHAPTER 3: POPULATIION DYNAMICS OF LAYSAN ISLAND'S RESIDENT DABBLING DUCK

Chapter 3: ABSTRACT

Effective methods to estimate population size and reproductive success are essential to conservation planning for endangered species. I studied the parameters influencing the population dynamics of the Laysan teal (*Anas laysanensis*), an endangered island anatid of the Hawaiian Islands, currently restricted to an emergent atoll, Laysan Island. I marked 294 Laysan teal between 1998 and 2001 and used mark-resight methods to estimate population size and survival. Adult survival rates were high, 0.99-0.97 (SE<0.006), but duckling survival was much lower, varying from approximately 0.1 – 0.30 during 1998-2000. Carcass examinations indicated that most adults died of starvation and echinursis, and in contrast, most ducklings died of traumatic injuries. Estimates indicate the population density was high (between 546-827) from 1991 until August 1993, prior to a population crash that occurred between September and December 1993. The population has increased since the die-off to the most current (Sept-Nov 2001) size of 444 (SE 181) adults. Hatching success of 61 eggs was 48% and apparent nest success was 47% (19 nesting attempts monitored). Duckling mortality appears to be the most important limit to population growth, suggesting Laysan's capacity to support duckling broods is limited.

Chapter 3: Tables and Figures

CHAPTER 3: Population Dynamics of Laysan island's resident dabbling duck

Introduction

The Laysan teal is a non-migratory dabbling duck (Anseriformes: Anatini) endemic to the Hawaiian Islands. Compared with continental dabbling ducks, the species has reduced power of flight and other terrestrial adaptations (Livezey 1993). Though it can fly, it does not disperse from Laysan Island, where there are no mammalian predators. Sub-fossil evidence indicates that the species was previously widespread on the Hawaiian archipelago and its range contraction occurred between 1200-1500 ybp during the period of human colonization (Olson and James 1991, Cooper et al. 1996, Burney et al. 2001). The Laysan teal population underwent a major population bottleneck on Laysan Island after the introduction of European rabbits (*Oryctolagus cuniculus*) in 1911-1913. Dill and Bryan (1912) reported 12 total Laysan teal, a credible account of the total population size since there was no vegetation left on the island to conceal the birds (Moulton and Weller 1984). By 1923, the rabbits had devegetated the island, and most starved to death. A scientific expedition that year killed off the rest (Wetmore 1925). The Laysan teal miraculously recovered, but three other species of land birds went extinct: the Laysan millerbird (*Acrocephalus familiaris*), the Laysan apapane (*Himatione sanguinea*), and the Laysan rail (*Pozanula palmeri*).

The relict Laysan teal population is vulnerable to extinction from chance events such as severe weather, disease, accidental species introductions, or random catastrophes (Reynolds and Ritchotte 2002). The U.S. Fish and Wildlife Service (USFWS) lists the species as endangered and proposed recovery actions include the establishment of additional wild populations on other islands through translocation, and control of non-native mammalian predators (Reynolds and Kozar 2000a).

Though Laysan teal are sedentary and a geographically closed population, the species has been described as one of the most difficult birds to monitor in the Northwestern Hawaiian Islands (Sincock and Kridler 1977). This difficulty stems from their nocturnal habits, reluctance to flush, and tendency to hide in the bunch grass. Line transect methods disturb other bird species on Laysan Island, and tend to underestimate the population size because many Laysan teal are undercover diurnally (Sincock and

Kridler 1977, Moulton and Weller 1984, Marshall 1992a, Chapter 2). Nesting success and duckling survival also are difficult population parameters to estimate. Nests are well concealed, broods can be secretive, and brood mixing is common, thus confusing estimates of brood loss.

Marshall (1992b) and others determined that the best way to monitor the adult population size is by calculating marked to unmarked ratios at the island's interior lake at dusk. However, direct lake counts were used to index the population size in the last century and as recently as 1991-1998. Direct lake counts are not an effective method to estimate population size, because there is seasonal and environmental variability in use of the lake by Laysan teal. It is not possible to determine how the direct count relates to the total population size without perennial data from a marked population.

An alarming adult die-off due to starvation, parasite infestation by *Echinuria uncinata*, and reproductive failure occurred in 1993 during drought conditions on Laysan (USFWS data, David and Hunter 1994). The waterfowl parasite causes tumor-like nodules on the proventriculus, resulting in blockage and compaction of the digestive tract (Cornwell 1963).

The extent of the 1993 population decline was difficult to determine and alerted the USFWS to the need for more information on the species' population and basic biology. Clearly, a better understanding of the factors affecting survival and productivity is crucial for making management and conservation decisions affecting the Laysan teal. Here I report results of a study to estimate population size, adult and juvenile survival, reproductive success, mortality factors, and population variation from 1991-2001.

Methods

STUDY SITE

Laysan Island (hereafter Laysan) has the largest continuous land area of the Hawaiian atoll islands (Figure 1). Laysan lies 1463 km northwest of Honolulu, and is accessible only by boat (25º46' N, 171º44' W). This subtropical island is dominated by low herbaceous vegetation and contains an interior lake with mudflats (Ely and Clapp

1973). The lake is characterized by hyper-salinity and high nutrient content (Caspers 1981). Laysan is an important nesting colony for several million seabirds and is part of the Hawaii Islands National Wildlife Refuge Complex under the jurisdiction of the USFWS and the Coral Reef Ecosystem Reserve (USFWS 1982, NOAA 2001).

CAPTURE AND MARKING

Laysan teal were captured during moonless nights and predawn periods using a flexible handheld net (Fuhrman Diversified 3/8 x 54 net stick model A1-A/36 DC) and headlamps. I captured specific individuals before sunset using a noose carpet made from hardware cloth and 20-test monofilament (Bub 1991). Birds were trapped at the lake, in the vegetation, and around our camp during March-May 1998, October 1998-March 1999, May-June 1999, and March-July 2000. I banded and measured birds, and glued radio transmitters (glue-on 6-8 gm AVM model G3 and ATS model 2040) to some individuals. USGS numbered aluminum bands were placed on one leg, and Darvec plastic color-bands (Haggies Inc.), some with alpha or numeric codes, were applied to the other leg. All ducks were released within 10-30 minutes near their capture site. In the first year of marking birds (1998) anodized aluminum bands (Gey's Band and Tag, Inc) and wrap around plastic color bands (Avinet, Inc) were used. These faded or fell off and most were replaced with Darvec color bands in 1999-2001.

POPULATION MONITORING

Surveys

Once per week since 1991, USFWS field technicians and volunteers walked around the interior mudflat and counted all ducks visible around the lake, beginning one hour before sunset. Staff used binoculars, but did not record the band status of the birds until April 1998.

In March 1998 with initiation of my mark – recapture efforts, USFWS count methods were modified to record data on the band status of all birds counted: marked, unmarked, or unknown (i.e. legs not visible, or distant bird in bad light).
Color-bands were read weekly prior to sunset around the lake from March 1998 - Oct 2001, and twice per month at flocking areas on the coast from March 1998 - Oct. 1999

and March-July 2000. From Oct-Feb 2000 and from July-June 2001 resighting effort was reduced to twice per month around the lake. Observers noted the sex, age, and band combination of each bird.

Brood Monitoring

During the breeding seasons of 1998 and 2000, broods were checked daily around the lake using a spotting scope (Swarovski HD-AT80 40-60x zoom) and binoculars (10x40). In 1999, brood sightings were recorded incidentally, approximately four times per week. Hens were identified and all ducklings were counted and assigned to an age class based on plumage characteristics (see Gollop and Marshall 1954, Marshall 1989). Age categories included: stage I) the downy duckling stage from 1-18 days; stage II) ducklings in 'first feathers'; and stage III) the fully feathered pre-fledglings. Fledglings have a smaller eye-ring than after hatch year birds (AHY) and can be easily distinguished in the field from adults for 3-4 months after fledging (MHR pers. obs.).

Mortality Factors

All duckling and adult carcasses incidentally found on Laysan were collected and preserved by freezing or in 10% formalin. Carcasses were measured, given external examinations, and later submitted to a pathologist with the USGS National Wildlife Health Lab for necropsy (T. Work, DVM, USGS, Honolulu HI).

Data Analysis

ADULT SURVIVAL

Resighting data were divided into four periods representing typical intervals of the bird's annual cycle: March - May (laying, incubation, early brood rearing), June - August (early brood rearing, late brood rearing, molt), September - November (late molt, flocking, courtship, and pairing), and December - February (courtship and pre-breeding). Resighting effort during the last 6 months of 2000 and 2001 was reduced after our field work concluded. Therefore, longer time periods were used in the analysis (June - October, November - March, and April – June) for this interval.

Survival and detection probability can be estimated for multiple periods within a year. Adult survival (φ) and resight/recapture (p) probabilities were estimated over three-month time periods with Cormack-Jolly-Seber (CJS) models (Pollock et al. 1989, Lebreton et al. 1992) using program MARK (White and Burnham 1999). The estimate of survival is actually apparent survival, but because Laysan teal do not emigrate from the island, φ estimates actual survival for the time period. The compliment of apparent survival is apparent mortality, which accounts for both mortality and permanent emigration from the study area. During capture, both age: hatch year (HY); after hatch year (AHY); after second year (ASY); or after fourth year (AFY); and sex were assessed. This enabled estimation of survival and resight/recapture probabilities based on potential age and sex differences. Capture of HY birds took place after fledging, so the period of high mortality experienced by ducklings had already passed (see duckling survival below).

Candidate models were selected prior to the analysis (Burnham and Anderson 1998) based on available data and biological knowledge. The modeling approach was to first look at overall population survival models ignoring age and sex effects. The four models considered were: 1) constant (.) survival (φ) and recapture (p) or (φ(.)p(.)); 2) time-dependent (t) survival and constant recapture (φ(t)p(.); 3) constant survival and time-dependent recapture (φ(.)p(t)); and 4) time-dependent survival and recapture (φ(t)p(t)). Time variables were modeled as either constant over all periods or variable between all periods, which implies survival differs between periods of the year and not just between years. An additional model was constructed that allowed survival to vary between periods within the year but was constant for similar periods across years (*i.e.*, the March to May survival rates were different than the other three periods but the same for all March to May periods of 1998 to 2001).

Survival estimates considering age and sex variables were modeled as an additional effect to the overall survival model chosen above. Age-based and sex-based models were parameterized to contain separate structures for age or sex class survival (Pollock and Raveling 1982, Prevot-Julliard et al. 1998). Model selection was based on Akaike's information criterion (AIC; Akaike 1973, Burnham and Anderson 1998).

POPULATION ESTIMATES

The protocol for monitoring Laysan teal has remained constant since 1991 (see population monitoring above). The same three-month periods described previously for survival estimates were used to estimate population size. Population estimates were made based on detection probability obtained from census data collected on the marked population present in 1998 through 2001. This approach is based on the Lincoln-Petersen method (Pollock et al. 1990, Marshall 1992a) where the ratio of marked birds seen in a survey compared to the total number of marked individuals in the population is used to estimate the total population size. For the periods where marked to unmarked ratios are recorded (1998-2001), a standard Lincoln-Petersen model was used, and these estimates are compared to the detection probability estimates made for the same period.

Detection probability (*d*) for marked birds positively identified in the survey is the average number of marked birds seen in a given time period (*m*) divided by the total marked population (*M*):

$$\hat{d}_i = \frac{\bar{m}_i}{M_i}$$

Since multiple surveys were conducted within a time period, the average number of marked individuals seen within a given time period was divided by the total number of marked individuals in the population during the time period. The total number of marked individuals in the population at a given time, noted by subscript *i,* is an approximation based on the known number marked, minus the number of known mortalities. Unknown mortalities exist, but are likely negligible during short time periods. To account for the birds of unknown band status (unknown birds) counted during the surveys, the detection probability was modified according to the ratio of known to unknown birds in the survey by estimating the number of marked birds that are assumed to be in the unknown sample:

$$\hat{d}m_i = \frac{\bar{m}_i}{M_i}\left(\frac{n_i + n_i'}{n_i}\right) ;$$

where n_i is the total of known birds observed and n_i' is the number of unknown birds in the sample. From the marked data, three to four detection probabilities are estimated for each period, then averaged over a period (*i*), yielding the standard variance of a sample mean (Cassella and Berger 2002).

Using detection probabilities from 1998-2001, I estimated population size by calculating the average number of ducks seen for a given period, divided by the mean detection probability for that period, with the variance of a ratio (Seber 1982).

$$N_i = \frac{\bar{n}_i}{\bar{d}m_i}.$$

I assume that detection probability, which relates to the Laysan teal's breeding phenology, remains constant per period from 1991 to 2001. Although this assumption may be violated some years due to variation in breeding conditions, it does provide estimates that suggest population trends.

NEST MONITORING

I attached radio transmitters and tracked adult females during portions of the breeding season in 1998, 1999, and 2000 to locate nests and determine nest success. To prevent disturbance to nesting hens and reduce the risk of exposing nests to egg predators, such as the Laysan finch (*Telespiza cantans*), ruddy turnstone (*Arenaria interpres*), and bristle-thighed curlew (*Numenius tahitiensis*), nest contents were checked only if telemetry data suggested an incubation break, nest failure, or after the normal 29-30 day incubation period. Hatching success was determined by counting the number of egg shell membranes and unhatched eggs remaining. Eggs were counted at some active nests, but were not removed or handled to reduce risks of attracting finches. Because of these constraints, I report "apparent nest success" instead of Mayfield's daily survival rates for nests (Sargeant and Raveling 1992). If undiscovered nests were abandoned before the clutch was incubated (or between tracking sessions), this would have inflated our estimates of nest success and biased results.

DAILY SURVIVAL OF DUCKLINGS

I calculated the survival rate of broods associated with individually marked hens during 1998 and 2000. Intensive daily monitoring of individual broods was not feasible in 1999. Our estimates of survival include partial and total brood loss. Daily survival rates were estimated using a modified Mayfield procedure that allows for brood mixing within families (Flint et al. 1995).

The assumptions of the modified Mayfield model are that: 1) marked females with broods represent a random sample of the population; 2) females are monitored at regular intervals; 3) disappearances due to adoptions cannot be distinguished from disappearances due to death and both are equally observable; 4) the fates of individuals within broods are not independent of the brood; and 5) survival changes with the age of brood members (Flint et al. 1995). Estimated daily survival rate ($E\hat{S}Ri$) was calculated for each brood (i) associated with an identifiable female (Flint et al. 1995):

$$E\hat{S}R_i = 1-(\Delta BS_i/EXP_i)$$

Where ΔBS is the change in brood size and EXP is the duckling exposure days. Duckling exposure days are calculated as total days survived by individuals in the brood (Flint et al. 1995).

Although brood rearing areas were checked daily, not all broods were sighted, so an unstructured sampling schedule was applied to the survival model. Because juvenile waterfowl typically experience the highest mortality during the downy stage, I estimated survival for 2 age classes: days 1-18 (stage I) and 19-40 (stage II). I only included data from broods hatched before 5 June and first sighted at 1-8 days old. Late broods (after 5 June) were excluded from the analysis because crew changes in July prevented intensive monitoring of later broods.

FLEDGING SUCCESS

I monitored the total number of ducklings and new broods, including unmarked hens at least weekly during the 1998-2000 breeding seasons. Surveys to determine fledgling success were conducted within two months of the peak of fledging in September or October of 1998-2001. Because fledgling survival until SY is high, fledging success is similar to recruitment. Recruitment refers to the new birds entering the breeding population, often defined as the number of young females in the population divided by the total number of females (Cowardin and Blohm 1992). Because I cannot determine the sex of fledglings nor identify the unbanded recruits accurately by field marks, I instead estimated fledgling success as the ratio of birds of the year entering the population shortly after fledging divided by the total number of ducklings produced within a breeding season or cohort (*x*) as an index of duckling survival to post-fledging ($\hat{S}PF$):

$$\hat{S}PF_x = \frac{n_{tx+1}}{n_{tx}}$$

where $\hat{S}$PF is the proportion of individuals (*n*) surviving to t+1 or fledging (Krebs 1999) with 95% binomial confidence limits (Zar 1999). I assumed that the ducklings and fledglings from a cohort were equally observable in the brood rearing areas at the lake. This assumption may have been violated, especially during the first two days after hatching, when some hens with broods are secretive, and duckling loss before reaching brood rearing areas would be undetected. If fledglings were more easily detected than ducklings, the consequence of this violation is a bias towards higher estimated fledgling success.

RESULTS

ADULT SURVIVAL

Two hundred and ninety-three ducks were banded with individually identifiable leg bands and monitored from 1998 to 2001. AIC model selection procedures identified the φ(t)p(t) model as the best choice to represent the overall survival and resight or recapture probabilities ($AIC_c = 4218$). Examination of parameter estimates revealed that the first nine periods had almost identical survival rates (0.984 to 0.997, SE < 0.006) and the last three periods were lower but similar to each other (0.967, 0.965, and 0.927 respectively). The second best model based on AIC was φ(.)p(t) ($AIC_c = 4242$). Based on evidence from these two models an intermediate model was parameterized that had constant survival for the first nine periods and a different constant survival for the last three (φ(2.)p(t). Resight/recapture rates were time dependent. AIC model selection criterion identified this new model as the best choice to represent the survival and recapture probabilities for Laysan teal ($AIC_c = 4212$). Estimated survival was 0.99 (SE = 0.001) over the first nine periods and was 0.97 (SE= 0.005) over the last three periods. Detection probabilities ranged from 0.56 to 0.91, except for the April to July period in 2001, which was lower at 0.33 (Table 1). Detections during this period were fewer than normal because observer effort and experience were less than for other periods.

Of the marked birds, 117 were males, 164 females, and 12 unknown, allowing for the addition of sex as a possible factor to the model, represented by a group effect, 'g'. AIC model selection criterion selected the φ (2 .)p (t) model over the φ (2 g) p (t) model. Examination of the group effect model gave a survival rate for the first nine periods of 0.993 (SE = 0.001) for males and 0.993 (SE = 0.002) for females, demonstrating the validity of the constant survival model over the sex effect model. Ages were known for 253 AHY birds, 27 HY birds, and 13 AFY color banded birds. Most of the HY birds were captured during the latter part of this study, and sample sizes for AFY were small, thus age specific survival was insufficient to analyze.

Recoveries were not included in the survival model because too few adult carcasses were found. Enumeration methods indicate that only one of 27 HY birds marked in 1999 and 2000 was recovered as a SY carcass. Two of 15 AFY birds detected in 1998 but first banded in 1993 and 1994 were recovered as carcasses in June 2001. Eight of 297 AHY or ASY birds marked between 1998 - 2000 (0.027 95% CI 0.018-0.039) were recovered by Oct. 2001 lending support to our model (φ)t(p)t estimates of survival for this age class. Additional data are needed to verify higher mortalities indicated by enumeration for HY (0.037 95% CI 0.003-0.176) and AFY (0.133 95% CL 0.10-0.142) for all periods combined 1998-2001.

ADULT POPULATION ESTIMATES

The number of marked ducks used to estimate detection probability ranged from just over 100 in the initial periods to 308 by 2000. Modified detection probability ranged from a low of 0.245 (SE= 0.0236) in the June-August period to a high of 0.656 (SE = 0.1126) in the September-November period (Table 2). The June-August surveys in 2001 were omitted from the estimation of detection probability and considered as outliers due to inexperienced observers. The total number of ducks observed during the lake counts demonstrates a similar pattern between the time periods (Figure 2). The number of ducks observed in September-November and December-February during 1991 and 1992, the first two years of standardized population monitoring by the USFWS appear high, which may represent over-estimates for these periods. I suspect that during the early periods of population monitoring, juvenile birds were not distinguished from adults, resulting in higher adult counts. Regardless, the total count reflects high total population density (adults and juveniles) prior to the population crash that occurred in 1993 during the drought.

Population estimates range from a high of 827 (SE 365) birds in June-August of 1993 to a low of 82 (SE 71) birds in March-May 1994 (Table 3, Figure 3). The 1993 population crash actually occurred after the June-August period and was seen in the estimates starting in September of 1993. During the March-May period, the population was initially estimated at 535 individuals, declined to less than 100 by 1994, and has since been increasing steadily every year, with the exception of 1998, a drought year distinguished by high reproductive failure. The current (2001) population size is estimated to be 444 (SE 181) adult birds.

NEST MONITORING

In 1998, an El Nino drought year, no nests were found. Seven of 13 hens retained radios and were tracked for more than 25 days during the 1998 nesting season (March - May). One hen nested and produced ducklings in May after her transmitter detached in April 1998. In 1999, 16 of 24 hens retained radio transmitters for more than 30 days during the nesting season (February - June), and 11 nests were found. Eight of these nests were discovered within the first 3 days of incubation. Three active nests were checked during incubation breaks. Ten of the 11 nests contained eggs, and 50% of nests with eggs hatched ducklings. Clutch sizes varied from 1-6 eggs, with a mean of 3.8. Of 38 eggs found, 17 (45%) hatched successfully (Table 4). One radio tagged hen produced three ducklings before the nest was located, and another (failed) nest could not be relocated to check the eggs, after an island crew change.

In 2000, ten of 15 hens retained radios for more than 30 days during the nesting season (April-June) and seven nests were found. Four of these were checked for egg counts during incubation breaks. One radio tagged hen produced four ducklings, but her nest was not located. Clutch sizes varied from 1-6; the mean clutch size was again 3.8. Six of the seven nests found contained eggs, and 50% of those with eggs hatched a duckling. Of the 23 eggs found, 12 (52%) hatched successfully (Table 4). "Apparent" nest success was 47%. That is, 9 of 19 known nesting attempts hatched at least one duckling.

DUCKLING SURVIVAL

In 1998, ten broods were observed and the mean brood size observed was 2.6 (SD 1.4) for day old ducklings (N=8 broods) and 2.5 (SD 1.7) at day 40 (N=2). The apparently similar size broods at day 1 and day 40 are not high survival, but due to brood amalgamation. Mean brood size, typically reported as an indicator of brood success, is less useful in a creching species. However, if total brood losses are included, the mean brood size decreases to 0.9 (SD 1.66) at day 19 and 0.5 (SD 1.27) at day 40. The daily rate of survival ($D\hat{S}R$) was 0.77 (SD 0.31) for stage I ducklings, and 0.90 (SD 0.86) for stage II ducklings (Table 5). In 2000, the mean brood size observed was 3.2 (SD 1.58) for day old ducklings (N=19 broods), and 2.4 (SD 3.72; N= 44 broods) for 19-day old ducklings (Stage II). Mean brood size increased to 4.4 (SD 3.2) by day 40, again due to duckling adoptions (N=11). The $D\hat{S}R$ was 0.91 (SD 0.19) for stage I ducklings and 0.95 (SD 0.11) for stage II ducklings. $D\hat{S}R$ underestimated stage survival compared with fledgling success estimates (below), perhaps because brood mixing, adoptions, and complete brood losses make individual broods difficult to follow.

Fledging Success

Survival of ducklings to post-fledging ($\hat{S}PF$) was 0.10 (95% CL 0.03-0.28) in 1998, 0.29 (95% CL 0.25-0.34) in 1999, and 0.29 in 2000 (95% CL 0.25-0.34). The mean ratio $\hat{S}PF$ for 1998-2000 was 0.28 (95% CL 0.21 to 0.36). $\hat{S}PF$ is not dependent on tracking individual broods, and is supported by the population estimates derived from mark-resight methods. Number of ducklings, broods, and fledglings from sighting data 1998-2000 are given in Figure 4.

Causes of Mortality

Data from carcasses incidentally collected in 1993 and 1998-2001 reveal that factors contributing to adult and juvenile mortality were quite different. Of the 45 carcasses suitable for examination, cause of death could be determined definitively in 33 cases; the remaining 12 cases represent educated guesses (Figure 5). Most adult mortality was due to starvation combined with *E. uncinata* infestation. An adult female was found egg-bound and suffering echinurisis. Two adults were found dead from starvation (no sign of nematodes) and one adult died of bacterial encephalitis (Dr. T. Work, DVM, USGS data). Moulton and Weller (1984) reported adult mortality by sexual attack and seabird collision during 1978-79 studies, but no adult carcasses from 1993 or 1998-2001 exhibited any signs of trauma.

Most ducklings, in contrast, died of traumatic injuries. Aggression has been observed towards ducklings by non-breeding adult teal, and rarely by hens with broods towards a duckling not belonging to her. Stray ducklings are often bit or charged if they approach a non-parent (MHR pers. obs.). One such attack was suspected to cause duckling mortality (Boswell and Keitt 1995). Attacks on ducklings by adult ducks have been reported in other species in crowded habitats where food may be limited (Pienkowski and Evans 1982). Ducklings are also susceptible to trauma by albatross and other large seabirds, which are abundant on Laysan. In 1992, USFWS field staff found 10 ducklings with crushed skulls. Greater frigate bird attack was suspected as the cause of death (Newton and Chapelle 1992).

Of the 27 duckling carcasses suitable for examination, seven exhibited no obvious signs of trauma, starvation, or disease; these deaths were attributed to exposure to adverse weather. Duckling mortality has been ascribed to exposure of ducklings separated from the brood, especially during rainstorms (Moulton and Marshall 1996). Few ducklings died of echinurisis, starvation, or pneumonia (Dr. Thierry Work, DVM, USGS data; Figure 5).

Mortality trends

Brood monitoring data and age structure of carcasses found incidentally (n = 86) between 1998-2000 reveal that the downy stage is the most vulnerable, especially during the first six days after hatching. Most carcasses (76%) found were ducklings in the downy plumage stages less than 18 days old (Figure 6). Duckling carcasses from 1998-2001 were found mostly in the spring and summer after the peaks of duckling hatching. Of the carcasses recovered in 1998-2001, adults comprised 16% of the specimens, 57% of which were females. Most adult carcasses from those years were found in mid to late summer after the peak of breeding. Adult carcasses during the 1993 die-off were found from August 1993 to January 1994 (USFWS data, Darnall and White 1993, Bauer and Gauger 1994).

DISCUSSION

Survival is a principal parameter shaping population dynamics and is equally important for understanding the evolution of life history characteristics in waterfowl (Johnson et al. 1992). Laysan teal, like many island endemics, show K-selected traits: low adult mortality and low recruitment compared to continental species (Lack 1970, Weller 1980). It is essential to understand factors that drive annual survival of sex and age classes to manage threatened and endangered species. Compared with other waterfowl, the Laysan teal has very high adult survivorship for both sexes (Table 6). Limited data from recoveries suggest that post fledging survival is also high.

The Laysan teal's nesting biology on Laysan is understudied, but we know that reproduction is highly variable and that clutch sizes are small. Our nest monitoring data were limited due to small sample sizes, but results indicate that apparent nest success is similar to that reported for many North American dabbling ducks (Sargeant and Raveling 1992; Table 7). I believe radio telemetry and cautious nest checks helped minimize bias often associated with apparent nest success. Previous studies of Laysan teal underestimated nest success (11% in 1980) due to human disturbance during active nest checks, inflating egg predation rates by Laysan finches (Moulton and Weller 1984). The cause of nest failure in the North American species is largely predation, whereas causes for nest failure during this study are speculative or unknown, since few active nest checks were made. I need to determine whether nest success is limited by competition with Laysan finch for sites, avian egg predation, or inbreeding depression. A more intensive nesting study would help resolve these uncertainties.

Pre-fledgling waterfowl are particularly vulnerable to mortality. Despite the importance of the pre-fledgling period to the dynamics of waterfowl populations, brood biology is the most poorly understood aspect of waterfowl ecology (Sedinger 1992). Few studies estimate duckling survival to fledging, and mortality rates are highly variable (Sargeant and Raveling 1992). Mortality rates of mallard ducklings from numerous studies ranged from 0.56-0.66, and mortality was attributed mainly to predation and exposure (Sargeant and Raveling 1992, Mauser et al. 1994). The importance of nutrition to duckling mortality is more difficult to assess, and has probably been underestimated (Sedinger 1992).

Duckling survival on Laysan is low, and is a primary demographic parameter limiting population growth. Our model of daily survival of ducklings from sightings data of hens with marked broods may have underestimated survival. Although I assumed the data met the assumptions of Flint et al.'s (1995) model, disappearances due to adoption and death may not be equally observable. The pervasive mixing of broods (0.47 of hens cared for ducklings from other broods), high incidence of complete brood loss, and the large proportion of unmarked hens in the population may have also hindered the model's accuracy. A radio telemetry study of hens with ducklings or individually tagged ducklings would improve estimates of daily survival. Otherwise, identification of new broods, total counts of ducklings, and fledgling success provide an estimate of duckling survival, which can be substantiated with the post-breeding population estimates.

Evidence from duckling carcasses on Laysan indicate that trauma due to over-crowded brood rearing habitat, followed by exposure were important mortality agents for downy stage ducklings, particularly from 1-6 days of age. Brood separation can lead to exposure especially in stage I ducklings, which have underdeveloped capacities for thermoregulation. On Laysan, many conditions may lead to brood separation: crowded conditions, seabird and human disturbance, plus long distance or frequent movements to suitable brood rearing habitats.

El Niño Southern Oscillation (ENSO) events can disrupt normal rainfall patterns, causing droughts in some years. In 1993, during a period of high population density, Laysan experienced its worst drought in twenty years. Lake levels shrank to their lowest levels since 1973 (USFWS data). The drought and epizootic of 1993 had catastrophic impacts on the population, resulting in adult mortality as high as 0.75. ENSO events in 1987, 1993, and 1998 also resulted in reproductive failure (Marshall 1989, USFWS data, MHR data). Differences in duckling survival in 1998 verses 1999 and 2000 were likely due to the drought conditions in 1998 which influence food and water abundance (Chapter 2), along with female and duckling body condition. Laysan teal carcasses are rarely found; thus, few causes for adult or duckling mortality have been identified in the past.

Prior to 1923, a brackish water permanent pond occurred southwest of the lake, but was filled by the shifting sands caused by the rabbit infestation of the early 1900's (Ely and Clapp 1973). Other freshwater seeps were likely degraded or filled by the shifting sands. Fresh and brackish water seeps surround the lake and serve as drinking areas for finches, shorebirds, and waterfowl. Hens used these, emergent vegetation, and ephemeral wetlands as brood nurseries (A. Marshall pers. obs, MHR data). Management to restore freshwater seeps should be investigated. Habitat restoration may create additional brood rearing habitat, reduce crowding and duckling mortality due to trauma. Management could be beneficial during severe droughts or to improve duckling survival to provide more fledglings for proposed translocations.

Population counts from September-November and December-February had the highest detection probabilities. Typically, birds have completed molting and nesting during these months and are more likely to be seen, yielding the highest numbers of lakeside teal for annual population estimates, yet the resight models can be applied to any time period. Resight models based on marked to unmarked ratios are ideal for estimating population size and sex ratios in this geographically closed population. The only drawback is that future population estimates require a portion of the population be marked periodically, because estimates become less accurate as marked birds die-off. Marking Laysan teal requires skilled personnel and is labor intensive.

Direct lake counts do not provide a population estimate and are of no value during the breeding and molt (March-September). Direct lake counts *do* provide a rough index of population status during the post-molt and pre-breeding periods (October-February), but are not recommend for a population monitoring program if a marked population can be maintained.

Inter-related factors govern Laysan's teal's population growth: weather, food resources, wetland condition, and inter and intra-specific population density on Laysan Island. The population was believed to be self-regulating at approximately 400-600 adult birds (Moulton and Marshall 1996); yet random or consecutive disasters such as the 1993 El Nino drought and epizootic or the rabbit introduction of the 1903, are likely to prevent the population's persistence. Viability models for small populations of isolated species predict a high risk of extinction due to stochasticity (Shaffer 1981, Caughley 1994).

Evidence suggests that prehistoric populations on the main Hawaiian Islands were adversely affected by introduced mammalian predators, rats (*Rattus exulans*) in particular (Burney et al. 2001). Habitat destruction or degradation, and hunting also contributed to Laysan teal declines (USFWS 1982). Alien species, indirectly harmful to the historical Laysan and/or extirpated Lisianski populations, include rabbits, mice, invasive weeds, and possibly predatory insects (Warner 1963, Olson and Ziegler 1995). Storms, drought-related food reductions, disease, and the island's limited carrying capacity are among the factors limiting the Laysan population. Duckling mortalities in 1999-2000 suggest the lack of sufficient brood rearing habitat on Laysan. Long-term threats include sea level rise due to global warming. Inbreeding depression may be a limiting factor; however, I lack the evidence to evaluate this possibility.

The Laysan teal population is likely to become extinct without intervention, and monitoring is essential for guiding the species' management and recovery. More information is needed on factors that influence reproductive success, hatchability, and brood survival. A strategy to restore species viability is to maintain the population on Laysan and establish additional populations other islands (Sincock and Kridler 1977, Aldrich 1980, Reynolds and Ritchotte 2002), at sufficient numbers that each population is resistant to demographic and environmental uncertainties (Reynolds and Ritchotte 2002).

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Table 1. Survival and recapture estimates with standard errors and 95% confidence intervals.

Parameter	Estimate*	Standard error	95% Confidence Interval Lower	Upper
φ(1 to 9)	0.99	0.001	0.992	0.996
φ(10 to 12)	0.97	0.005	0.956	0.975
p(2)	0.68	0.041	0.59	0.75
p(3)	0.91	0.025	0.85	0.95
p(4)	0.86	0.026	0.80	0.90
p(5)	0.78	0.026	0.73	0.83
p(6)	0.56	0.029	0.51	0.62
p(7)	0.79	0.023	0.74	0.83
p(8)	0.56	0.029	0.50	0.61
p(9)	0.78	0.025	0.72	0.82
p(10)	0.78	0.023	0.74	0.83
p(11)	0.68	0.029	0.62	0.73
p(12)	0.33	0.030	0.27	0.39
p(13)	0.87	0.048	0.75	0.94

* for the intermediate model: constant survival for 2 time period poolings (φ(1 to 9) and φ(10 to 12) with time dependent resight-recapture or (φ (2 .) p(t)).

Table 2. Estimated detection probability of marked birds and modified detectability using four periods within a year. Standard errors are given in parentheses.

	Mar-May	June-Aug	Sep-Nov	Dec-Feb
Known Detectability[1]	0.15 (0.03)	0.13 (0.014)	0.22 (0.02)	0.12 (0.02)
Modified Detectability[1]	0.30 (0.03)	0.25 (0.02)	0.66 (0.11)	0.47 (0.07)

[1] Detection probability is estimated from resight data obtained during 1998 to 2001 and modified by the proportion of observed birds with unknown band status.

Table 3. Population estimates from 1991 to 2001 using four periods within a year. Standard errors are given in parentheses.

Year	Mar-May	June-Aug	Sep-Nov	Dec-Feb
1991		440 (332)	546 (142)	620 (262)
1992	426 (255)	487 (508)	537 (130)	484 (209)
1993	535 (249)	827 (365)	143 (86)	88 (36)
1994	82 (71)	88 (114)	92 (45)	114 (122)
1995	197 (70)	167 (175)	260 (117)	133 (77)
1996	124 (106)	84 (33)	269 (94)	191 (136)
1997	100 (68)	140 (152)	294 (117)	306 (143)
1998	398 (95)	402 (121)	261 (97)	285 (133)
1998 L-P[1]	321 (42)	350 (66)	293 (93)	214 (96)
1999	237 (64)	162 (62)	297 (106)	330 (103)
1999 L-P	293 (131)	358 (184)	258 (73)	448 (217)
2000	375 (183)	413 (139)	367 (110)	354 (224)
2000 L-P	300 (149)	224 (47)	361 (160)	505 (243)
2001	394 (300)	216 (116)	444 (181)	
2001 L-P	389 (158)	496 (222)	522 (256)	

[1] Lincoln-Petersen estimates (L-P) from years when banding was conducted.

Table 4. Nesting success summaries of Laysan teal from radio tracking studies

Summaries	1998	1999	2000	1998-2000 Summary	1979-1980 (Moulton and Weller 1984)
Nests found with eggs	0	10	6	16	9
Nesting attempts[1]	0	11	8	19	9
Successful nests[2]	NA	5	4[3]	9	1
Nests of radio tagged hens	0	10	7[3]	17	7
Radio tagged hens monitored ≥ 25 days during peak nesting season	7	16	10	33	8
Eggs found	0	38	23	61	31
Mean clutch size	NA	3.80	3.83	3.82	3.4
Eggs scavenged or depredated	NA	8	1	8	ND
Nests scavenged or depredated	NA	2	1	2	7
Partially hatched eggs[4]	NA	0	2	2	0
Infertile or undeveloped eggs	NA	4	6	10	3
Unknown or abandoned eggs (nests)	NA	5(1)	3(0)	8(1)	3
Hatched eggs	NA	17	12	29	2
Re-nest attempts of (initially) radio tagged birds same breeding season	NA	2	0	2	0
Age of nester					
ASY	NA	11	5	18	ND
SY	NA	0	2	2	ND
Radio tracked hens w/ broods after radio detachment	1	9	ND	10	NA

[1] Incubation behavior was indicated by tracking data; however, eggs were never produced at one of the nest sites

[2] At least one egg hatched as indicated by eggshell membrane or ducklings observed.

[3] One nest of a radio tagged hen was never located.

[4] Fully formed ducklings (2 of 6) did not complete hatching, possibly abandoned due to asynchronous nest hatch

Table 5. Observed changes in brood sizes of marked Laysan teal and estimated daily survival (SD) of Laysan teal ducklings in 1998 and 2000.

Variable	1998		2000	
	Stage I [1]	Stage II [2]	Stage I	Stage II
Total duckling exposure days	202.5	141	1698.5	2134
Broods observed	10	3	52	27
Estimated D$\hat{S}$R includes	0.77	0.90	0.91	0.95
TBL[3]	(0.31)	(0.10)	(0.19)	(0.11)

[1] 1-18 days of age

[2] 19-40 days of age

[3] TBL = total brood loss (includes all known broods)

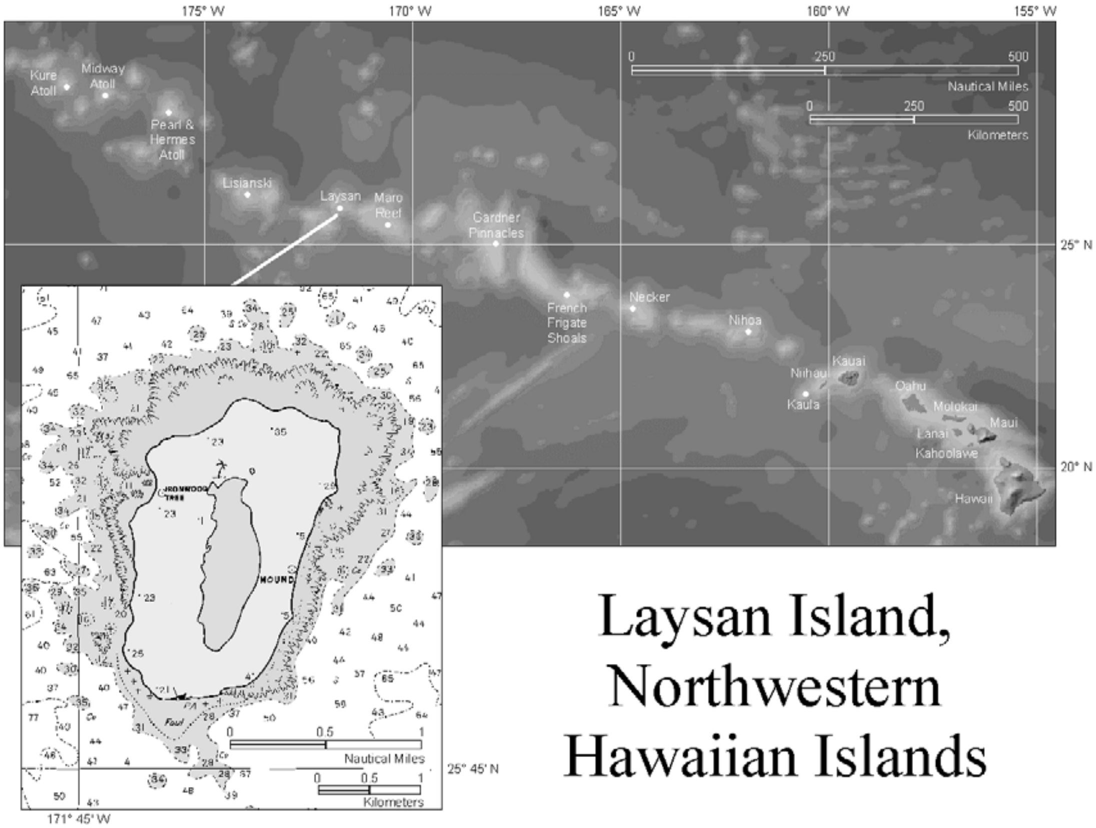
Table 6. Adult survivorship estimates from other waterfowl species.

Species	♀ Avg. annual survival (SE)	Reference
Black duck, *A. rubribes*	0.45 (0.39)	Krementz et al. 1987
Brown teal, *A. chlorotis* [1]	0.63	Williams & Dumbell 1996
Green-winged teal, *A. crecca*	0.51 (0.06)	Chu et al. 1995
Laysan teal, *A. laysanensis*	0.98 (0.01)	This study
Pacific grey duck, *A. superciliosa*	0.55 (0.12)	Caithness et al. 1991
Mallard, *A. platyrhynchos*	0.59 (0.07)	Trost 1987
Nene, *Brant sandvicensis*	0.87 (0.04)	Banko et al. 1999

[1] All post fledged birds

Table 7. Examples of apparent mortality rates of waterfowl nests.

Species	Nests/ yrs	Morality (range)	Primary cause	Habitat/location; Reference
Black duck	590/10	0.54(0.29-0.70)	predator	Estuary/Quebeca; Reed 1975
Laysan teal	19/2	0.47(0.45-0.50)	unknown	Grassland/Laysan; This study
Mallard	213/4	0.57 (0.48-0.62)	predator	Grassland/Manitoba; (Dzubin and Gollop 1972)
Nene	363/35	0.66 (0.44-0.75)	predator	Subalpine/Hawaii; Banko et al. 1999



Laysan Island,
Northwestern
Hawaiian Islands

Figure 1. Map of Hawaiian Islands, with detail of Laysan Island.

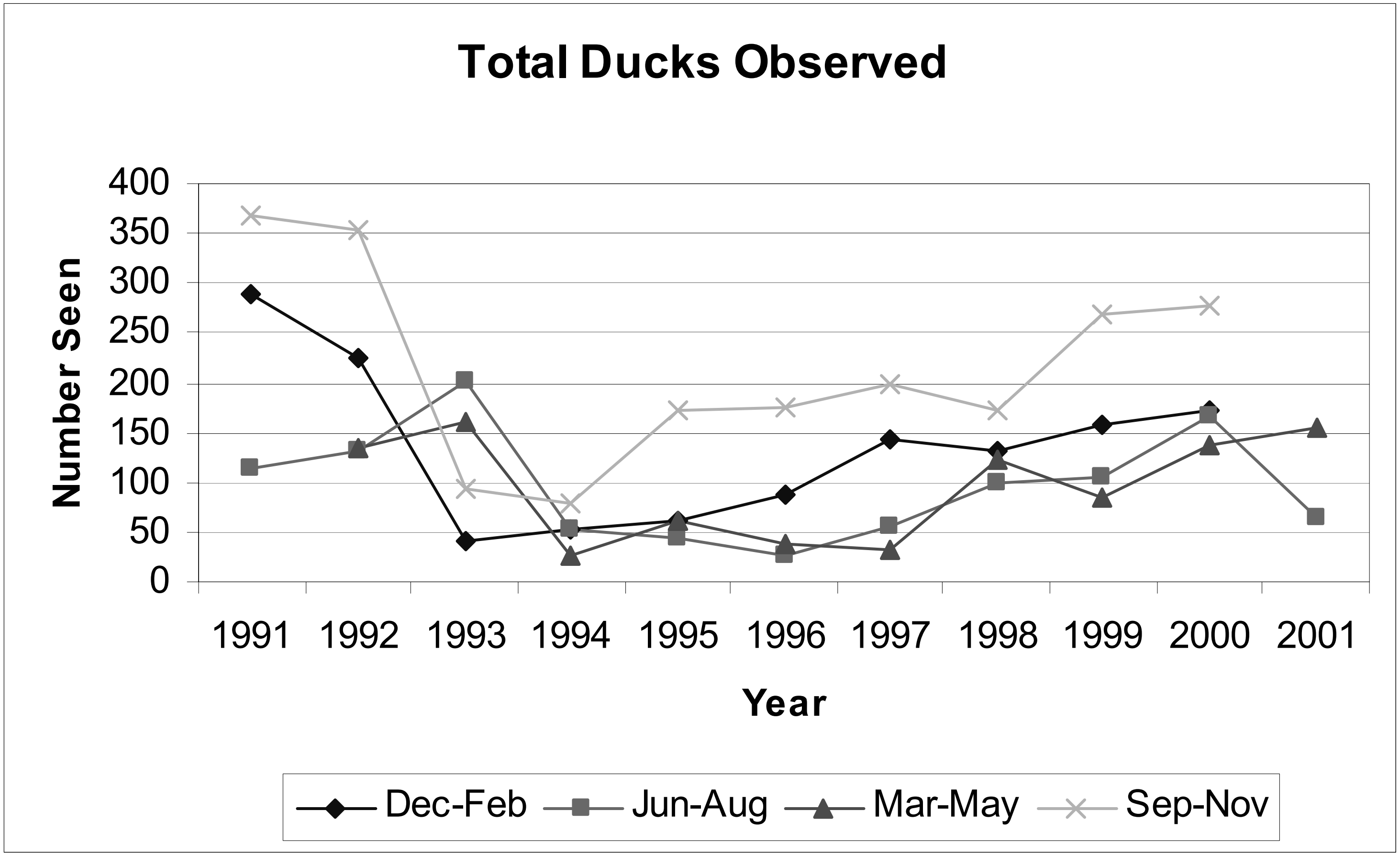


Figure 2. Total Laysan teal observed during lake counts made from 1991-2001.

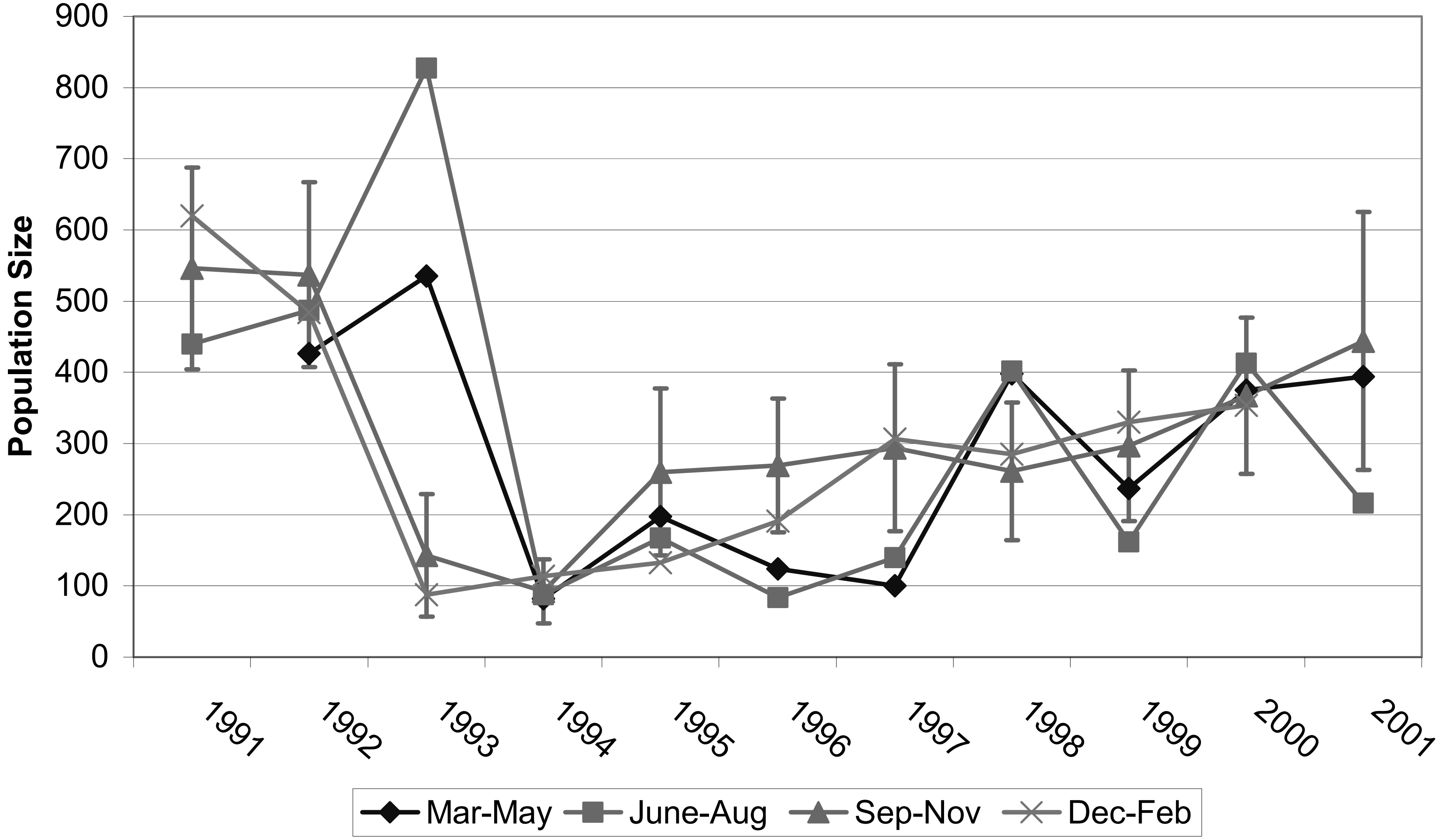


Figure 3. Population estimates for the Laysan teal 1991-2001.

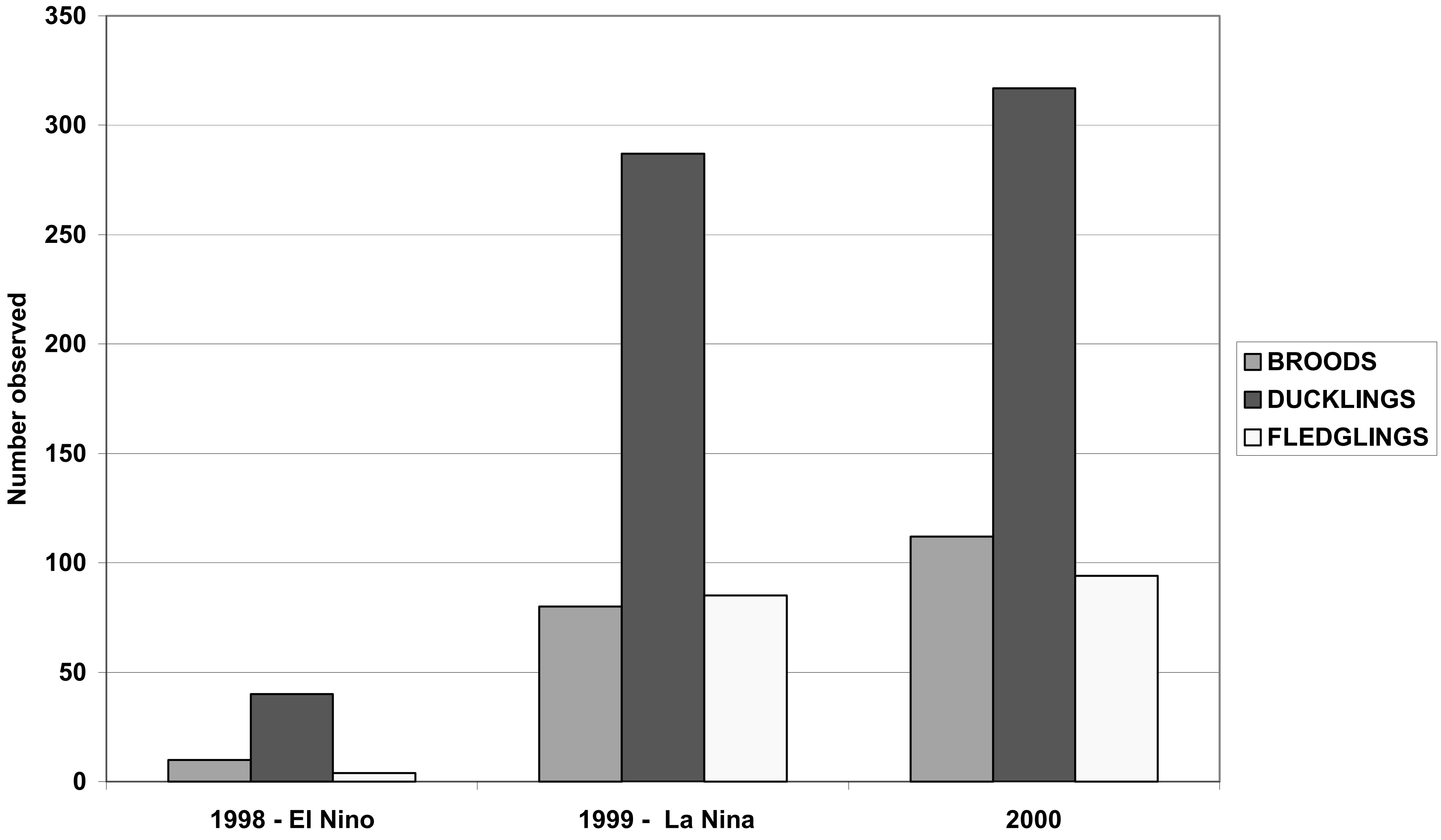


Figure 4. Reproductive success from sightings data 1998-2000.

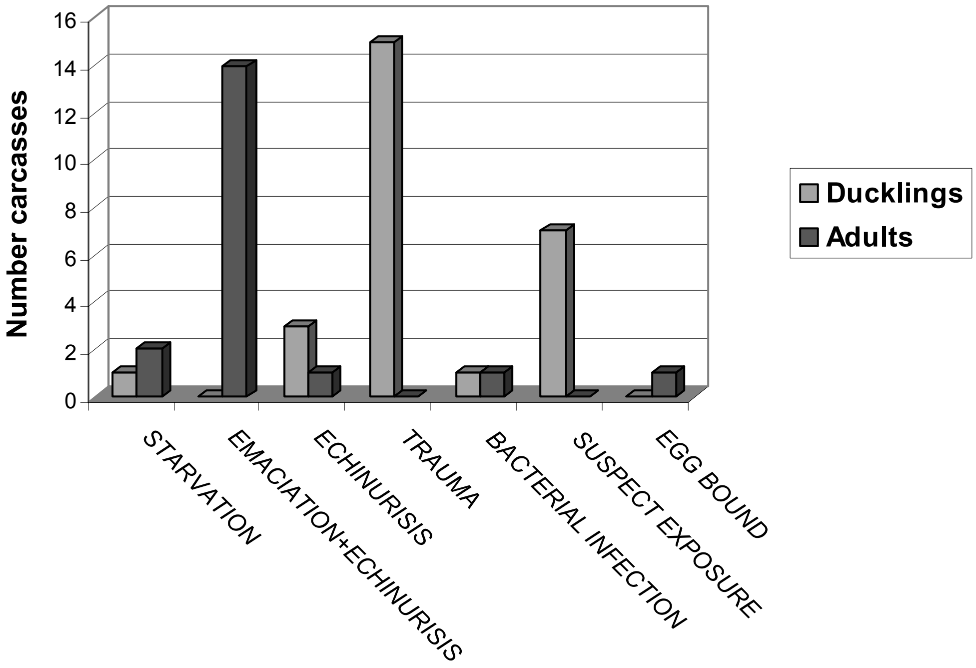


Figure 5. Causes of death determined for 45 Laysan teal carcasses suitable for examination out of 105 collected in 1993 and 1998-2001.

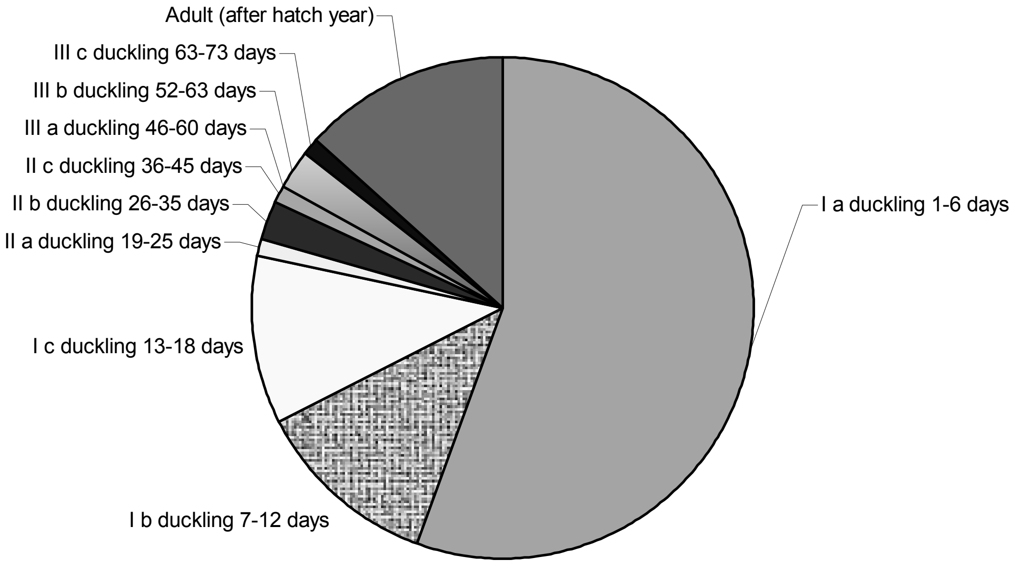


Figure 6. Age classes of Laysan teal carcasses recovered 1998-2000 (n=86).

CHAPTER 4: HABITAT USE AND HOME RANGE OF THE LAYSAN TEAL ON LAYSAN ISLAND, HAWAII

Chapter 4: ABSTRACT

I studied the 24 hr habitat use and home range of the Laysan teal, a Hawaiian endemic dabbling duck, using radio telemetry during 1998-2000. Radios were retained for a mean of 40 days (0-123 d; N=73 adult birds radio tagged). Daily habitat use comparisons were made for birds with ≥ 7 locations per tracking session. Most birds showed strong evidence of selective habitat use by time of day (63-94%). Most adults preferred the terrestrial vegetation (88%), and avoided the lake and wetlands during the day. At night, 63% of the birds preferred the lake and wetlands. Nocturnal habitat use differed significantly between the non-breeding and breeding seasons. The lake and wetland habitats were used more frequently during the non-breeding season. Most individuals showed strong site fidelity during the tracking period, but habitat selection varied between individuals. Mean home range size was 9.78 ha (SE 2.6) using the fixed kernel estimator (95% kernel; 15 birds with >25 locations). The average minimum convex polygon size was 24 ha (SE 5.6). The mean distance traveled was 178 m (SE 30.5) ranging from 0-1649 m during tracking periods that ranged from 31-121 days (mean duration 75 days).

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CHAPTER 4. Habitat use an home range of the Laysan teal on Laysan Island, Hawaii

Introduction

The Laysan teal, *Anas laysanensis,* is a non-migratory anatid (order: Anseriformes) currently restricted to the 415 ha of Laysan Island National Wildlife Refuge, a coral atoll (25º 46’N 171º 44’W;USFWS 1982). The species is federally endangered and occurs as a single relictual population. Laysan teal were previously widespread across the Hawaiian archipelago, but were extirpated from the main Hawaiian islands around 1500 ybp, and from Lisianski Island (26° 04’ N 173° 58’ W) about 150 ybp (Olson and Ziegler 1995). For details on the species biology, see Moulton and Marshall’s (Moulton and Marshall 1996) species account and the preceding chapters. For information on the landscape, historical, physical, and biological features of Laysan Island (here after ‘Laysan’) see Ely and Clapp (1973) and Rauzon (2001).

Today, the Laysan teal shows strong tenacity to Laysan and successful dispersal from the island is unknown. Mating arrangements, parental care, and the distribution of resources are major elements influencing the spatial use of waterfowl (Oring and Sayler 1992, Anderson and Titman 1993). The mating system of the Laysan teal is characterized by annual monogamy with re-pairing, and some long-term pair bonds (Moulton and Weller 1984, Oring and Sayler 1992, MHR data). Females provide the incubation and care of precoccial young. Previous researchers (Moulton and Weller 1984) radio tracked eight hens and seven drakes in 1980, and described the birds’ widespread use of the island. However, the Laysan teal’s habitat use, movements, and home range have never been systematically described or quantified.

Refuge managers are interested in restoring ecosystems of the Northwestern Hawaiian islands, particularly Laysan (Morin and Conant 1998), however little is known about the Laysan teal’s habitat use. Wild translocation, or the movement of wild birds to establish new populations, has been proposed to reduce the species’ high extinction risks (see Chapter 1; Aldrich 1980, Reynolds and Kozar 2000). Information on the species range of resource use on Laysan will provide insights into its ecology, and may provide insights as to the suitability of translocation sites with respect to those resources. To provide details on the species habitat use and home range, I systematically radio tracked Laysan teal during 24 hr periods during breeding and non-breeding seasons of 1998-2000.

Methods

HABITAT USE

I classified Laysan into to four general habitat zones used by the Laysan teal. The 'coastal zone' encompassed area below the high surf zone, or sparsely vegetated coastal or dune areas on the outer perimeter of the interior bunch grass association. The 'camp zone' included all areas within 60 m of man-made structures and storage areas associated with the camp. The 'lake zone' consisted of all wetland plant associations, mudflats, ephemeral wetlands, and the lake. The 'terrestrial zone' included most of the interior of the island excluding all wetlands and the camp (Figure 1). I determined relative habitat use by capturing and attaching radio transmitters to a sample of birds, and systematically tracking the distribution of these individuals among the habitat zones of Laysan.

Radio tracking

I captured Laysan teal during moonless nights and predawn periods from March–May 1998, Oct 1998-March 1999, May-June 1999, and March-July 2000, using a handheld net and headlamps. Some individuals were captured before dark using a leg noose carpet (Bub 1991). Banding, morphometric measurements, and transmitter attachment took 20-30 min. Birds were processed and released within 60 m of their capture site. I placed a USGS numbered aluminum band on the tibiotarsus of one leg and applied a Darvec™ plastic color-band to the other leg and sealed it closed with laminating glue. Birds weighing greater than 400 g were fitted with 6-8 gm radio transmitters (AVM model G3, ATS model 2040). I attached transmitters with Tessa™ tape and Skin Bond™ surgical glue. A small patch of feathers was cut on the bird's mid-back and gauze was applied with surgical skin bond adhesive to the area similar to methods described by

Raim (1978). Transmitters were ‘super-glued’ to the gauze, and then several strips of tape were used to adhere the transmitter to adjacent uncut feathers (Figure 2).

Radio locations were determined via homing (Samuel and Fuller 1996), using hand held antennas (Telonics 3-element Yagi) and Telonics TR-2, TR-4 and AR-8000 receivers. I recorded the habitat zone of all telemetry locations, and plotted confirmed locations on a map between April-July 1998, 1999, 2000, and November 1998-March 1999. Radio tracking was divided into 4 sessions from approximately 0400–0830 hrs (morning session), 0900-1530 hrs (day session), 1600-2030 hr (evening session), and 2100-0300 (night sessions). I recorded one location per individual per session. Birds were not tracked during consecutive sessions so that locations could be considered independent (or to reduce the effects of autocorrelation). I attempted to determine locations of all birds equally per time session, but variable radio retention rates and personnel constraints prevented a completely balanced design. Detection type (signal received and visually confirmed), behavior, habitat use, and time of detection were recorded, and 20 min focal observations of behavior were collected when feasible (see Chapter 2).

Analysis

Individual animals were identified and habitat use was measured for each; the availability of habitat zones was estimated for the entire study area (Laysan). From this, I applied habitat selection indices (Manly et al. 1993) to test the null hypothesis that birds utilized habitat in proportion to availability. From the locations of the radio tagged birds, I can describe individual habitat use in relation to habitat availability. Habitat selection models estimate a resource selection probability function based on proportional estimates of used and available resources (Krebs 1999):

$$w_i = \frac{o_i}{p_i}$$

where w_i = Habitat selection indices for habitat i

o_i = Proportion of habitat used by individuals

p_i = Proportion of habitat available in the environment (estimated)

Resource ratio indices, w_i , of 1.0 indicate habitats are used in proportion to availability; above or below 1.0 indicate disproportional habitat use, i.e. "selected" or "not selected" respectively. Resource indices are statistically significant if the confidence intervals for w_i do not contain the value zero (Manly et al. 1993).

I also calculated standardized selection ratios (B_i), which estimate the probability that a randomly selected habitat unit will be used next, if habitats were equally available. Standardized ratios are less sensitive to the effects of large but rarely used resource categories, and are recommended by Manly et al. (1993):

$$B\,i = \frac{w_i}{\sum w_i}$$

where Bi = standardized selection index. Values less than 1, divided by the number of resources, indicate no preference and values above or below indicate preference and avoidance, respectively (Manly et al. 1993).

To test the null hypothesis that the Laysan teal are using habitat randomly, G-tests were used (Krebs 1999):

$$X^2 = 2\sum_{i=1}^{n} [u_i \ln (u_i/Up_i) + m_i \ln (m_i/(m_i+u_iM/U+M))]$$

where X^2 = the chi-square value (df = n-1),

u_i = the number of observations of use per habitat i,

m_i =the number of observations of available habitat i,

U = the total of observations of use,

M = the total observations of availability, and

n = the number of resource categories.

Standard errors and confidence limits are given by Manly et al. (1993). Bonferroni corrections were used for multiple comparisons. Assumptions of the analyses are that 1) the habitat availability does not change during the study period, 2) available and used resource units were correctly identified, 3) birds sampled have free access to all habitats, 4) relocations of radio tagged individuals are sufficiently spaced in time to assume each is an independent habitat point (Krebs 1999), and 5) that animals are more likely to use the most available resource (Luigi and Fuller 2000).

I used permutation analysis to test for seasonal and yearly differences in habitat use during each time session (SAS version 8.02). The breeding season included March-July 1998, 1999, and 2000, and the non-breeding season included October –February 1998-99. Some individuals bred early (i.e. a few birds were gravid in February), and were grouped with the breeding birds for analyses. Separate tests were run for each time session. The p-value for the permutation procedure is given by the rank of the chi square test on the original data relative to the permutated data (Manly 1997) calculated as:

$$\frac{\text{rank}}{(5000+1)};$$

Where “1” is added for the data value. Bootstrap procedures were used to select 1000 samples from the data to recompute the proportions of habitat use and estimate standard deviations. Z-statistics were used to test for differences between the mean season-year combinations (Zar 1999).

Home range calculations

I used minimum convex polygons (MCP) and fixed kernel home range estimators to describe extent of area utilized and probability of use, by the radio tagged individuals (GIS; Arc view ERSI Inc; Millspaugh et al. 1998). Least square cross validation was applied to select bandwidths for smoothing parameters with minimum estimated error (Seaman et al. 1999). Estimates were calculated using the Animal Movements Extension (Hoodge and Eichenlaub 1997). Sample size requirements (minimum locations needed) per individual for home range analysis were based on visual assessments of scatter plots for grid counts (ha used) vs. locations collected.

RESULTS

I attached radios to 73 Laysan teal over the course of this study, three of which were given radios in two different years (Appendix 1). Between 14-23 individual ducks were tracked per field season, and tracking efforts were initiated within 48 hours of deployment. Radio retention varied between individuals and seasons, averaging 40 days

(0-123 d; Table 1 and Appendix 1). Degraded surgical glue resulted in poor radio retention in late May and June of 1999. Sixty-two birds were tracked more than twice (1601 locations), of which 53 were tracked during all four tracking sessions with 10 or more locations recorded (1562 locations). Eleven transmitters detached shortly after deployment or failed. Unrecovered transmitters, lost shortly after initial attachment, were likely lost in the lake. Fifteen birds with more than 25 mapped locations were selected for home range analysis.

Individual habitat use

The amount of time spent in each of the different habitat zones varied among individuals (N= 52). Three individuals spent most of their time in the camp, others visited briefly, and many never visited camp at all. Individuals that used the coastal zone only made brief visits. On average, birds spent most of their time in the terrestrial zone followed by time spent at the lake (Figure 3).

I tested for evidence of non-random habitat use, by time of day, using chi-squared log-likelihood statistics and constructed Bonferroni confidence limits for individual habitat selection ratios. Habitat availability is based on estimates by Morin (Morin 1992) and new calculations of island area based on satellite imagery (IKONOS 18Dec2001; Table 2). Only birds with seven or more locations per tracking session are included. Although repeat locations from the same radio-tagged individual are considered unavoidably "dependent", these data met the assumption of independence in respect to sufficient time interval between an individual's locations (Manly et. al 1993, Millspaugh and Marzluff 2001).

In the morning, 63% of the birds (7 of 11) used the habitat zones in disproportion to what is expected by chance, providing evidence of "preference" or "avoidance" for some habitat zones. One bird selected the camp habitat and three selected the terrestrial zone in discordance with availability. The remaining birds did not use the camp or coastal zone, and used the lake and terrestrial zones in proportion to availability (Table 3a). In the day, 94% of birds (15 of 16) used habitat zones in unexpected proportions. Fourteen birds (88%) "preferred" the terrestrial zone and "avoided" the lake (Table 3b). Two individuals preferred the camp.

During the evening, all habitat zones were utilized and 68% of the birds (13 of 19) showed evidence of habitat selection. The same two birds preferred the camp (11%), five preferred the lake (26%), and three preferred the terrestrial zone (16%). Five birds (26%) used the coast, however coastal habitat use was less than would be expected, based on its availability (Table 3c; also see Seasonal habitat use). At night, 94% of the birds (16 of 17) showed evidence of habitat selection. One bird preferred the camp (6%), 10 preferred the lake (63%), and one preferred the terrestrial zone (6%). The remaining birds did not use the camp or coastal zone but used the lake and terrestrial zones in proportion to its availability (Table 3d).

Seasonal habitat use

Tracking data were summarized by season and year to examine seasonal effects of habitat use during 1998-2000 (N=62 birds; Figure 4). The lake and terrestrial zones were used heavily in all years according to the diurnal pattern described above. During a period of continuous tracking from November 1998-July 1999, I observed an increase in time spent in the camp zone. Although this habitat use shift is not evident from the radio-tagged birds in 2000, data from resighted color-banded individuals suggest that time spent in camp by some birds (i.e. "camp ducks") increased from early spring to mid summer.

Coastal zone use was rarely detected during months with radio telemetry (less than 1% of total locations per month). However, an increase in the frequency of coastal sightings was evident from incidental sightings and circum-island surveys by USFWS field staff during the post-breeding season (i.e. October-November; Table 4), a period when few birds had been radio-tagged (Appendix 1). Flocks of up to 70 adult and hatch year (HY) Laysan teal were recorded on the coast during this time. The tide pools at the south end of Laysan were a principal flocking area. Laysan teal did not forage on the coast but bathed, loafed and courted (Chapter 2). Most coastal detections during the post-breeding season occurred during the hour before sunset, and observations indicated that birds flew inland at sunset (MHR pers. obs., USFWS data).

A permutation analysis based on chi-square statistics was used to test for significant heterogeneity in seasonal habitat use (SAS version 8). A separate analysis was run for each time session and the chi-square distributions were permutated 5000 times. Seasonal habitat use differences occurred during the night session (X^2 =140.29, P=0.0002; Table 5).

The proportions of habitats used were calculated for each individual during the nocturnal tracking session. Boot strapping procedures (N=1000) were used to estimate mean proportions and standard errors of habitat used (Manly et al. 1997). Results indicate habitat use in the lake and terrestrial zone varied significantly during the non-breeding season compared with the breeding seasons (Table 6). Z- test were used to compare the sample means (Zar 1999). Radio-tagged adult birds used the lake zone significantly more during the non-breeding season than the breeding seasons ($P<0.001$), and used the terrestrial zone less during the non-breeding season compared to the breeding seasons ($P< 0.01$). The breeding seasons (typically March-June/July) showed similar habitat use patterns during 1998, 1999, and 2000. However during the breeding season of 1998, an El Nino drought year, birds spent less time in the terrestrial zone nocturnally than in the subsequent breeding seasons of 1999 and 2000 (Table 6), though these differences were not significant at the 95% level (Table 7).

HOME RANGES

The movements of 15 adult radio tagged birds, 10 females and 5 males with 586 mapped locations were analyzed for home range estimates (Table 8). Capture locations and radio recovery locations (if known) were included in the calculations. Home range estimates (95% kernel) averaged 9.7 ha (SE 2.6). Core areas of use (50% kernel) averaged 3.2 ha (SE 1.45). Minimum convex polygon (MCP) estimates describe the areas encompassed by movements and averaged 24 ha (SE 5.6; Table 8). Mean distance traveled during tracking durations of 31-121 days was 178 m and ranged from 0-1649 m. There were no correlations between home range size and tracking duration (Pearsons correlation =-0.05, p=0.85) or between the number of radio locations (Pearson's correlation =0.021, p=0.61) and home range. Individuals exhibited considerable variation in home range size (Figure 5 and 6). All of the radio tagged birds were observed with mates during radio tracking, with the exception of one unpaired male (No. 123; Figure 6). This bird's home range was four times larger than the paired adults' ranges.

Six of the 10 “home range” females nested during the period in which they were tracked, however none with successful nests retained their radios during brood rearing. The data from resighting records indicate that some females with broods shift their habitat use patterns to include the lake zone diurnally. Hens with broods also appear to shift their core areas of use to include freshwater seeps within the lake zone for brood rearing. For example, in 2000, female 144 (radio tracked in 1999) was resighted at least 52 times from Jan-Sept. She nested in camp, and before and after brood rearing, 86% of the sightings were in camp (18 in camp, 1 at the coast, 2 at the lake). During brood rearing, all sightings (N=31) were at the lake and included morning, day, and evening sightings. After her ducklings fledged, she returned to camp without them (MHR data).

I found no significant differences (α=0.05) in the home range estimates between males and females (2 sample t-test; t=-0.92; df = 4; p=0.411) or between the breeding and non-breeding season estimates (t=-1.0; p=0.351; df=7). Although the non-breeding season home ranges were slightly larger, I cannot make a distinction between seasonal differences and individual variation with limited sample size. Small sample sizes (number of individuals) prevented statistical comparisons between years, and radio retention limited comparisons of individuals between seasons.

DISCUSSION

The results from tracking radio-marked individuals showed differences in habitat use by time of day, with a few birds appearing to “specialize”. At least two individuals preferred the camp, and two preferred the terrestrial zone during all time periods.

The importance of the terrestrial zone for diurnal cover, nesting, and nocturnal foraging was highlighted in Chapter 2, and habitat selection indices should be considered within the context of the activities that take place within a habitat. The lake zone, used for drinking, foraging, and other activities, was typically avoided diurnally by all except hens with broods. Adults that did use the lake by day spent most of their time there foraging (44%), whereas only 4% of their diurnal activity in the terrestrial zone was dedicated to foraging (Chapter 2). None of the birds preferred the lake zone during the day, however many preferred the lake at other times. All individuals with large numbers of radio locations ($\geq$7 per time sessions) used the lake zone at least once.

The camp area appears to attract birds because of the food and water available there, and a few individuals might be considered camp “specialists”. The coast was rarely used during our tracking efforts, but may be important on Laysan seasonally for bathing, flocking, and courtship activity during the period after molt when pairs reunite. The widespread use of the island was documented previously by Moulton and Weller (1984), however they reported “intense” use of the lake by adult pairs. In contrast, I found that more time was spent in the terrestrial zone, and that many individuals used the lake infrequently.

During the breeding season, duck’s spent less time at the lake during the nocturnal tracking session. These differences maybe a result of shifts in foraging behavior in response to prey abundance or due to breeding behavior. Nest site selection, territorial defense (if it exists), and incubation by females would certainly contribute to greater time spent in the terrestrial zone, and less time foraging at the lake during the breeding season. Yet in 1998, none of the radio tagged females nested or incubated during the tracking period, and indeed tracking indicated more time in the terrestrial zone at night, compared with the non-breeding season. During nocturnal trapping, I found and captured many more birds in the terrestrial zone during the 1998 drought than during subsequent years. Fifty percent of the captures were from the terrestrial zone during the breeding season of 1998 compared with 2% during the non-breeding season, 4% in 1999, and 6% in 2000 (MHR data). Most of these terrestrial captures were made while the birds were foraging. This suggests that seasonal differences in habitat use are influenced by both nesting and foraging. Unfortunately, nocturnal behavioral observations from the terrestrial zone were insufficient for seasonal comparisons (Chapter 2).

We have much to learn about the relationship between home range size, quality (resource availability), social systems, and fitness in waterfowl (Nudds and Ankney 1982). Variation in home range sizes is thought to be due to spatial and temporal variability in resources, and the “defendability” of crucial resources (Nudds and Ankney 1982). The question of territoriality is complex, and Moulton and Weller (1984) believed that Laysan teal did not establish exclusive feeding territories (i.e. defendable), however their evidence was not presented, and may have applied only to the lake. Nest sites or other terrestrial resources may be defended during the breeding season and “loose territoriality” may exist. Another possibility is that dominance hierarchy is important to acquire and maintain vital resources (Anderson and Titman 1993) on Laysan. Active Laysan teal around the lake spent over a quarter of their time in antagonistic, social, or courtship activities during behavioral observations (Chapter 2). To understand the role of the “home range” and the fitness consequences of resource and space use by this species, long-term field studies of the role of social relationships, the impact of seasonal variability and density dependent changes in habitat use are needed.

Home range estimates of Laysan teal provide valuable baseline information on individual variability in habitat use and movements on Laysan Island during the period between 1998-2000. Most paired adults had small home ranges (< 10 ha) and very small core areas of use (< 2 ha). Unpaired birds and hens with broods are likely to use larger home ranges or shift their core areas of use. Future home range comparisons and habitat use of birds translocated to different islands and habitats may prove useful, especially if we can relate these to body condition and breeding success.

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Table 1. Radio transmitter retention estimates[1] 1998-2000.

Season of attachment	N	Mean days	Range	SD
Breeding 1998	14	24.14	0-79	25.83
Non-breeding 1998-1999	20	44.90	21-84	20.36
Breeding 1999	23	48.00	0-123	38.26
Breeding 2000	16	43.88	0-94	27.11

[1] Radio retention days are conservative and based on the last day that birds with radios were confirmed. In some cases, tracking effort ended before radios detached.

Table 2. Estimates of habitat available on Laysan Island

Habitat zone	Area available (ha)
Camp	3
Coast	118
Lake	104
Terrestrial	190
Island	415

Table 3a. Morning habitat selection indices (*w*) and standardized indices (B) of radio-tagged Laysan teal with $\geq$7 locations (N) from 1998-2000. Confidence intervals (95%) with Bonferroni corrections are given in parentheses. Chi-square log-likehood statistic (*X^2*) tests the null hypothesis of random habitat use.

		CAMP		COAST		LAKE		TERRESTRIAL		X^2	P
Bird	N	*w*	B	*w*	B	*w*	B	*w*	B	*df 3*	value
22 ♀	10	0	0	0	0	2.0(0.36-3.63)	0.65	1.10(0.22-1.97)	0.35	7.66	0.05*
25 ♀	7	0	0	0	0	0.57(0-1.89)	0.23	1.87(1.11-2.64)†	0.77	6.32	0.10
70 ♀	11	0	0	0	0	1.09(0-2.45)	0.41	1.59(0.83-2.35)	0.59	7.78	0.05*
75 ♀	9	76.85(19.6-134)†	0.98	0	0	0.89(0-2.28)	0.01	0.49(0-1.24)	0.01	34.49	<0.01*
179♀	9	0	0	0	0	0.89 (0-2.28)	0.34	1.70(0.94-2.46)	0.66	6.94	0.73
239 ♀	8	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	12.32	<0.01*
282 ♀	8	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	12.32	<0.01*
82 ♂	12	0	0	0	0	1.66(0.20-3.12)	0.57	1.27(0.48-2.07)	0.43	8.34	0.04*
143 ♂	7	0	0	0	0	2.28(0.35-4.21)	0.7	0.94(0-1.96)	0.30	6.12	0.10
148 ♂	10	0	0	0	0	2.39(0.77-4.02)	0.73	0.87(0.02-1.73)	0.27	9.21	0.03*
157 ♂	8	0	0	0	0	1.50(0-3.23)	0.52	1.37(0.41-2.32)	0.47	5.47	0.14

† Indicates strong evidence of habitat selection. Resource indices are statistically significant if the confidence intervals for w_i do not contain the value zero (Manley et al. 1993).

* Indicates X^2 statistical significance of non-random habitat use at the α=0.05 level.

Table 3b. Day-time habitat selection indices (*w*) and standardized indices;(B) of radio-tagged Laysan teal with $\geq$7 locations (N) from 1998-2000. Confidence intervals (95%) with Bonferroni corrections are given in parentheses. Chi-square log-likehood statistic (X^2) tests the null hypothesis of random habitat use.

		CAMP		COAST		LAKE		TERRESTRIAL		X^2	P
Bird	N	*w*	B	*w*	B	*w*	B	*w*	B	*df 3*	value
6 ♀	10	0	0	0	0	0.4 (0-1.35)	0.17	1.97 (1.39-2.55)†	0.83	10.14	0.02*
22 ♀	15	0	0	0.23(0-0.80)	0.01	0.27(0-0.91)	0.11	1.89(1.35-2.43)†	0.79	10.69	0.014*
70 ♀	16	0	0	0	0	0	0	2.18(1.89-2.48)†		24.30	<0.01*
75 ♀	12	115.28(78.1-152.5)†	0.99	0	0	0.33(0-1.13)	0.003	0.18(0-0.62)	0.002	71.54	<0.01*
144 ♀	9	123(86.8-159.2)†	0.99	0	0	0	0	0.24(0-0.82)	0.002	61.76	<0.01*
149 ♀	10	0	0	0	0	0.40(0-1.35)	0.65	1.97(1.39-2.55)†	0.35	10.14	0.02*
173 ♀	7	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	10.8	0.01*
179 ♀	17	0	0	0	0	0	0	2.18 (1.89-2.48)†	1.0	26.56	<0.01*
239 ♀	16	0	0	0	0	0.25(0-0.86)	0.11	2.05(1.62-2.48)†	0.89	18.17	<0.01*
282 ♀	7	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	10.8	0.01*
82 ♂	12	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	18.35	<0.01*
123 ♂	11	0	0	0	0	0.36(0-1.23)	0.15	1.99(1.44-2.53)†	0.88	11.45	<0.01*
132 ♂	8	0	0	0.44	0.19	0	0	1.91(1.22-2.60)	0.81	7.31	0.06
143 ♂	10	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	15.35	<0.01*
148 ♂	17	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	25.77	<0.01*
157 ♂	9	0	0	0	0	0	0	2.18(1.89-2.48)†	1.0	13.84	<0.01*

† Indicates strong evidence of habitat selection. Resource indices are statistically significant if the confidence intervals for w_i do not contain the value zero (Manley et al. 1993).

* Indicates X^2 statistical significance of non-random habitat use at the α=0.05 level.

Table 3c. Evening habitat selection indices (*w*) and standardized indices; (B) of radio-tagged Laysan teal with $\geq$7 locations (N) from 1998-2000. Confidence intervals (95%) with Bonferroni corrections are given in parentheses. Chi-square log-likehood statistic (X^2) tests the null hypothesis of random habitat use.

Bird	N	CAMP		COAST		LAKE		TERRESTRIAL		X^2 *df 3*	P value
		w	B	*w*	B	*w*	B	*w*	B		
6 ♀	13	0	0	0	0	1.84(0.41-3.27)	0.61	1.17(0.41-1.95)	0.39	9.41	0.02*
22 ♀	12	0	0	0.59(0-1.54)	0.19	1.66(0.20-3.12)	0.52	0.91(0.12-1.70)	0.29	1.95	0.59
25 ♀	13	10.64(0-40.41)	0.83	0	0	0.31(0-1.05)	0.02	1.84(1.25-2.45)†	0.14	15.35	<0.01*
32	11	0	0	0	0	2.54(1.00-4.08)	0.76	0.79(0-1.59)	0.24	10.95	0.01*
70 ♀	11	0	0	0	0	0.73(0-1.89)	0.29	1.79(1.11-2.46)†	0.71	9.00	0.03*
74 ♀	8	0	0	0	0	2.49(0.71-4.28)†	0.75	0.82(0-1.76)	0.25	7.81	0.05*
75 ♀	17	65.1(23.3-106.9)†	0.98	0.21(0-0.71)	0.003	0.23(0-0.81)	0.004	0.90(0.24-1.56)†	0.014	47.11	<0.01*
144 ♀	11	113.18(73-153.4)†	0.99	0	0	0.36(0-1.23)	0.003	0.20(0-0.67)	0.002	64.86	<0.01*
173 ♀	9	0	0	0.39(0-1.31)	0.13	1.33(0-2.92)	0.45	1.21(0.30-2.13)	0.41	1.74	0.63
179 ♀	9	0	0	0	0	0.89(0-2.26)	0.34	1.69(0.94-2.46)	0.66	6.93	0.07
239 ♀	11	0	0	0	0	0.36(0-1.23)	0.15	1.99(1.44-2.53)†	0.85	11.45	<0.01*
282 ♀	15	0	0	0	0	1.60(0.29-2.90)	0.55	1.31(0.60-2.02)	0.45	10.26	0.02*
82 ♂	13	0	0	0	0	3.07(1.74-4.40)†	0.86	0.50(0-1.15)	0.14	17.74	<0.01*
121 ♂	6	0	0	0	0	3.33(1.65-5.0)†	0.61	0.36(0-1.20)	0.39	9.84	0.02*
123 ♂	7	0	0	0	0	3.42(1.92-4.93)†	0.92	0.31(0-1.03)	0.08	12.20	<0.01*
132 ♂	7	0	0	5.02(0-1.67)	0.15	2.28(0.35-4.21)	0.67	0.62(0-1.56)	0.18	3.27	0.35
143 ♂	11	0	0	0.32(0-1.08)	0.10	1.81(0.27-3.36)	0.58	0.99(0.16-1.82)	0.32	3.52	0.32

Bird	N	CAMP		COAST		LAKE		TERRESTRIAL		X^2 *df 3*	P value
		w	B	*w*	*B*	*w*	*B*	*w*	*B*		
148 ♂	11	0	0	0	0	1.45(0-2.93)	0.51	1.39(0.58-2.20)	0.49	7.47	0.06
157 ♂	8	17.29(0-64.73)	0.86	0	0	2.00(0.18-3.81)	0.10	0.82(0-1.76)	0.04	9.68	0.02*

† Indicates strong evidence of habitat selection. Resource indices are statistically significant if the confidence intervals for w_i do not contain the value zero (Manley et al. 1993).

* Indicates X^2 statistical significance of non-random habitat use at the α=0.05 level.

Table 3d. Night habitat selection indices (*w*) and standardized indices; (B) of radio-tagged Laysan teal with $\geq$7 locations (N) from 1998-2000.Confidence intervals (95%) with Bonferroni corrections are given in parentheses. Chi-square log-likehood statistic (X^2) tests the null hypothesis of random habitat use.

		CAMP		COAST		LAKE		TERRESTRIAL		X^2	P
Bird	N	*w*	B	*w*	*B*	*w*	*B*	*w*	*B*	*df 3*	value
6 ♀	13	0	0	0	0	0.92(0-2.10)	0.35	1.68(1.0-2.36)†	0.65	9.68	0.02*
22 ♀	12	0	0	0	0	2.66(1.19-4.13)†	0.79	0.73(0-1.48)	0.21	12.78	0.01*
32 ♀	14	0	0	0	0	2.85(1.50-4.20)†	0.82	0.62(0-1.29)	0.18	16.63	<0.01*
70 ♀	23	0	0	0	0	1.39(0.36-2.42)	0.49	1.42(0.85-2.00)	0.51	15.36	<0.01*
74 ♀	10	0	0	0	0	3.59(2.38-4.81)†	0.94	0.22(0-0.74)	0.06	19.48	<0.01*
75 ♀	13	63.85(16-111.6)†	0.98	0	0	0.92(0-2.10)	0.01	0.67(0-1.38)	0.01	38.66	<0.01*
149 ♀	14	0	0	0	0	3.99(3.14-4.84)†	1.0	0	0	37.41	<0.01*
173 ♀	15	0	0	0	0	3.72(2.71-4.74)†	0.96	0.15(0-0.50)	0.04	31.69	<0.01*
179 ♀	20	0	0	0	0	1.80(0.69-2.90)	0.60	01.20(0.59-1.81)	0.40	14.57	<0.01*
239 ♀	8	0	0	0	0	1.00(0-2.54)	0.38	1.64(0.77-2.50)	0.62	5.84	0.12
82 ♂	11	0	0	0	0	2.18(0.61-3.74)	0.69	0.99(0.16-1.82)	0.31	9.08	0.03*
121 ♂	12	0	0	0	0	3.66(2.55-4.77)†	0.95	0.18(0-0.62)	0.05	24.34	<0.01*
123 ♂	9	0	0	0	0	1.77(0.08-3.47)	0.59	1.21(0.30-2.13)	0.41	6.43	0.09
132 ♂	7	0	0	0	0	3.42(1.92-4.92)†	0.92	0.31(0-1.03)	0.08	12.20	<0.01*
143 ♂	15	0	0	0	0	3.45(2.32-4.60)†	0.92	0.29(0-0.77)	0.08	26.28	<0.01*
148 ♂	20	0	0	0	0	3.19(2.07-4.31)†	0.88	0.44(0-0.93)	0.12	29.04	<0.01*
157 ♂	14	0	0	0	0	3.71(2.66-4.75)†	0.96	0.16(0-0.53)	0.04	29.24	<0.01*

† Indicates strong evidence of habitat selection. Resource indices are statistically significant if the confidence intervals for w_i do not contain the value zero (Manley et al. 1993).

* Indicates X^2 statistical significance of non-random habitat use at the α=0.05 level

Table 4. Summary of Laysan teal sightings at the coastal zone during island walks 1998-2000 (USFWS data).

Month/yr	Birds/survey	Max. flock size/survey
Jul-98	1	1
Aug-98	5	5
Sep-98	1	1
Oct-98	38	63
Nov-98	66	70
Dec-98	29	69
Jan-99	16	36
Feb-99	2	2
Jul-99	0	0
Aug-99	1	3
Sep-99	7	24
Oct-99	13	35
Nov-99	27	56
Dec-99	1	6
Jan-00	15	10
Feb-00	15	23
Mar-00	4	7
Apr-00	5	10
May-00	4	4
Jun-00	0	0
Jul-00	1	1
Oct-01	47	46

Table 5. Results of permutation test: compares habitat use within the four season-year combinations; breeding 1998, breeding 1999, breeding 2000, and non-breeding 1998-1999 (N=62; 1604 locations).

Time	Chi-sq. test	Permutation P-value
Morning	34.49	0.06
Day	40.22	0.19
Dusk	41. 89	0.14
Night	140.29	0.0002*

* Indicates significant difference at the α=0.05 level

Table 6. Mean proportions and P-values of habitat use for seasons during the night sessions (bootstrap procedure N=1000).

Season	Camp	Coast	Lake	Terrestrial
Non-breeding	0	0	0.88 (0.03)*	0.12 (0.03)*
Breeding 1998	0	0	0.51 (0.10)	0.48 (0.10)
Breeding 1999	0.07	0	0.32 (0.56)	0.61 (0.06)
Breeding 2000	0	0	0.37(0.09)	0.63 (0.09)

* Indicates significant difference at the α=0.05 level

Table 7. Two sample Z-test of habitat use means for the night tracking sessions.

Habitat–season-yr	Non-breeding	Breeding 1999	Breeding 2000
Lake-breeding 1998	Z=3.89 P<0.0001*	Z=1.76 P=0.08	Z=1.06 P=0.29
Lake-breeding 1999	Z=8 P<0.0001*	---	---
Lake-breeding 2000	Z=5.46 P<0.0001*	Z=0.37 P=0.72	---
Terrestrial-breeding 1998	Z=-3.27 P=0.001*	Z=-1.0 P=0.31	Z=-1.04 P=0.30
Terrestrial-breeding 1999	Z=-6.96 P<0.0001*	---	---
Terrestrial-breeding 2000	Z=-5.23 P<0.0001*	Z=-0.20 P=0.83	---

* Indicates significant difference at the α=0.05 level

Table 8. Home range estimates (95% kernel), core use areas (50% kernel), and area encompassed by movements (100% MCP) of Laysan teal during 1998-2000. Data presented in hectares.

Dates[1]	Bird	N	Duration	95% kernel (ha)	50% kernel	MCP
98Mar15-Jun16	6♀	32	93	34.05	6.44	36.82
98Apr4-Jul17	25♀	26	104	4.78	1.24	17.02
99Jan12-Apr7	70♀	54	85	2.91	0.47	3.90
98Nov16-Dec17	74♀	27	31	11.13	1.51	18.47
99Mar7-Jul11	75♀	49	126	3.99	0.92	16.83
99Jun7-Jul11	144♀	26	34	2.41	0.88	9.78
98Dec20-99Feb05	173♀	37	47	33.23	4.93	47.10
99Jan13-Apr23	179♀	55	100	7.80	1.58	13.73
00Mar27-Jul12	239♀	39	107	4.24	0.41	7.02
00Apr19-Jun30	282♀	35	72	3.62	0.45	5.09
99Mar4-Jul3	82♂	48	121	15.71	3.80	48.72
98Nov17-Dec25	121♂	29	38	2.98	0.29	4.76
98Nov16-Dec24	123♂[2]	29	38	142.46	22.41	82.59
98Dec14-99Feb2	143♂	41	56	8.85	1.54	21.52
98Dec16-99Mar2	148♂	59	76	8.17	1.30	26.95

[1] Tracking dates include capture location and transmitter recovery location (if found).

[2] This bird was unpaired. All others were observed with mates during the tracking period.

Appendix

Appendix 1. Summary of radio tagged Laysan teal, tracking schedule, and individual radio retention from 1998-2000.

Season	ID of bird	Sex	Age	Attach date	Recovery date	Last date bird confirmed	Min. days on bird	Total detections	Percent visual detections	Tracking session[1]			
										A	B	C	D
Breeding 1998	6	F	AHY	15-Mar-98	25-Jun-98	11-May-98	56	39	48.72	3	10	13	13
	25[2]	F	AHY	04-Apr-98	05-Apr-98	04-Apr-98	0	1	100	1	0	0	0
	27[2]	F	AHY	04-Apr-98	15-Apr-98	09-Apr-98	5	4	75	1	2	0	1
	28[2]	F	ASY	05-Apr-98	09-Apr-98	05-Apr-98	0	1	100	1	0	0	0
	30[2]	M	AHY	05-Apr-98	13-Apr-98	11-Apr-98	6	1	100	0	0	1	0
	32	F	AHY	17-Apr-98	04-Jun-98	11-May-98	24	33	60.61	2	4	13	14
	34	F	ASY	17-Apr-98	01-May-98	21-Apr-98	4	21	60.67	2	1	5	13
	3	F	AHY	23-Apr-98	25-Jun-98	25-Jun-98	62	12	75	2	3	2	5
	55	F	AHY	23-Apr-98	18-Jun-98	26-May-98	33	13	69.23	2	2	4	5
	56	F	AHY	23-Apr-98	-----	04-May-98[3]	11	14	85.71	2	0	7	5
	25	F	AHY	28-Apr-98	-----	17-Jul-98[3]	79	20	95	4	3	12	1
	69	F	AHY	28-Apr-98	06-Jun-98	21-May-98	23	8	100	2	1	4	1
	70	F	AHY	28-Apr-98	18-May-98	28-Apr-98	2	4	25	0	1	1	2
	103[2]	F	AHY	18-May-98	25-Jun-98	22-Jun-98	35	5	20	0	1	3	1
Non-breeding 98-99	122	F	ASY	16-Nov-98	18-Dec-98	07-Dec-98	21	22	45.45	2	7	6	7
	123	M	AHY	16-Nov-98	28-Dec-98	22-Dec-98	36	30	60	4	10	7	9
	74	F	ASY	17-Nov-98	18-Dec-98	12-Dec-98	25	30	43.33	6	6	9	9
	121	M	ASY	17-Nov-98	26-Dec-98	17-Dec-98	30	30	50	6	6	7	11
	131	F	AHY	18-Nov-98	21-Dec-98	11-Dec-98	23	23	30.43	4	5	7	7
	132	M	AHY	18-Nov-98	21-Dec-98	20-Dec-98	32	24	54.16	2	8	6	8
	22	F	AHY	15-Dec-98	18-Jan-99	10-Jan-99	25	26	46.15	4	8	6	8

Season	ID of bird	Sex	Age	Attach date	Recovery date	Last date bird confirmed	Min. days on bird	Total detections	Percent visual detections	Tracking session[1]			
										A	B	C	D
Breeding 1999	143	M	ASY	15-Dec-98	-----	08-Feb-99[5]	53	42	66.67	7	10	11	14
	148	M	AHY	17-Dec-98	03-Mar-99	01-Mar-99[4]	74	57	57.89	10	17	11	19
	149	F	AHY	17-Dec-98	01-Feb-99	29-Jan-99	42	35	57.14	6	10	6	13
	152	F	AHY	18-Dec-98	18-Jan-99	11-Jan-99	23	22	45.45	4	5	4	9
	157	M	AHY	19-Dec-98	12-Feb-99	09-Feb-99[4]	50	38	57.89	8	9	8	13
	173	F	AHY	21-Dec-98	08-Feb-99	05-Feb-99[4]	44	40	57.50	6	8	9	17
	70	F	ASY	13-Jan-99	07-Apr-99	01-Apr-99[4]	78	56	48.21	11	15	10	20
	179	F	ASY	14-Jan-99	23-Apr-99	08-Apr-99[4]	84	54	48.14	9	17	9	19
	181	F	ASY	14-Jan-99	24-Feb-99	23-Feb-99[4]	39	27	62.96	4	10	5	8
	13	F	ASY	15-Jan-99	26-Feb-99	24-Feb-99[4]	39	32	53.12	6	7	8	11
	110	F	ASY	15-Jan-99	19-Apr-99	07-Apr-99[4]	82	53	52.83	11	13	11	18
	90	M	ASY	17-Jan-99	08-Mar-99	02-Mar-99[4]	45	40	42.50	6	9	8	17
	158	F	AHY	19-Jan-99	17-Mar-99	12-Mar-99[4]	53	45	80	11	10	8	16
	140[2]	F	ASY	15-Feb-99	22-Feb-99	21-Feb-99	6	0	NA	0	0	0	0
	171	M	AHY	15-Feb-99	03-Mar-99	02-Mar-99	17	13	69.23	3	2	3	5
	219	F	ASY	16-Feb-99	15-Apr-99	08-Apr-99	52	27	55.55	6	8	4	9
	54	M	AHY	05-Mar-99	15-May-99	07-May-99	62	25	52.0	7	8	5	5
	82	M	ASY	05-Mar-99	05-July-99	28-Jun-99	113	48	64.58	12	13	12	11
	75	F	ASY	08-Mar-99	12-Jul-99	11-Jul-99	123	50	64.0	9	12	16	13
	79	F	ASY	08-Mar-99	04-Jun-99	04-Jun-99	86	24	66.67	5	9	5	5
	232	F	ASY	08-Mar-99	1-Jun-99	21-May-99	73	18	27.78	4	6	2	6
	233	F	ASY	08-Mar-99	-----	03-May-99[5]	55	16	37.50	4	6	3	3
	238	F	ASY	09-Mar-99	03-May-99	26-Apr-99	47	15	40.0	4	4	3	4
	206	F	ASY	12-Mar-99	31-May-99	21-May-99	69	23	43.48	4	7	5	7
	228	F	ASY	12-Mar-99	-----	21-May-99[3]	69	10	50.0	3	2	4	1
	239[2]	F	ASY	12-Mar-99	29-Mar-99	25-Mar-99	13	4	75.0	1	2	0	1
	2	F	AHY	13-Mar-99	04-Jun-99	21-May-99	68	12	33.33	1	4	2	5

Season	ID of bird	Sex	Age	Attach date	Recovery date	Last date bird confirmed	Min. days on bird	Total detections	Percent visual detections	Tracking session[1]			
										A	B	C	D
	40[6]	F	ASY	13-Mar-99	22-May-99	10-May-99	57	11	100	2	1	8	0
	241	F	ASY	13-Mar-99	07-Jul-99	03-Jul-99	110	25	64.0	4	8	7	6
	246[2]	M	HY	22-May-99	-----	24-Jun-99[3]	0	6	100	2	1	3	0
	50[2]	F	AHY	23-May-99	01-Jun-99	24-May-99	1	4	25.0	1	0	2	1
	245[2]	F	ASY	23-May-99	-----	31-May-99[3]	8	3	100	1	0	2	0
	251	M	HY	24-May-99	-----	24-May-99[3]	0	3	100	1	0	2	0
	256	F	ASY	30-May-99	04-Jun-99	1-Jun-99	2	1	0	1	0	0	0
	257	F	ASY	30-May-99	-----	12-Jul-99[3]	42	21	90.47	6	3	6	6
	144	F	ASY	08-Jun-99	-----	09-Jul-99[3]	31	26	42.31	3	9	10	4
Breeding 2000	265	F	ASY	27-Mar-00	9-Jun-00	12-May-00	45	33	18.18	6	11	9	7
	239	F	ASY	28-Mar-00	12-Jul-00	02-Jul-00	94	38	28.95	7	14	11	6
	266[2]	F	SY	28-Mar-00	-----	20-Apr-00[5]	22	3	66.67	0	1	2	0
	270[2]	F	AHY	5-Apr-00	-----	5-Apr-00[5]	0	0	NA	0	0	0	0
	272[2]	F	ASY	05-Apr-00	-----	18-Jun-00[5]	73	8	50	1	3	3	1
	273[2]	F	SY	05-Apr-00	30-Apr-00	30-Apr-00	25	4	100	0	0	2	2
	274	F	SY	09-Apr-00	-----	08-May-00[5]	29	27	66.67	5	4	14	4
	275	F	SY	09-Apr-00	-----	05-Jun-00[5]	56	32	56.25	6	4	13	9
	277	F	SY	12-Apr-00	26-Jun-00	26-Jun-00	74	41	100	11	9	15	6
	50	F	AHY	14-Apr-00	15-Jun-00	21-May-00	37	29	34.48	7	5	11	6
	280	F	AHY	20-Apr-00	21-Jun-00	12-Jun-00	52	30	23.33	8	7	10	5
	282	F	SY	20-Apr-00	30-Jun-00	26-Jun-00	66	34	26.47	8	7	14	5
	22	F	AHY	25-Apr-00	08-Jun-00	08-May-00	13	23	17.39	6	7	6	4
	133	F	ASY	26-Apr-00	07-Jun-00	07-Jun-00	41	26	42.31	5	6	11	4
	311	F	SY	03-May-00	16-Jun-00	09-May-00	6	19	5.26	4	7	5	3
	151	F	ASY	14-May-00	-----	23-Jul-00[5]	69	13	53.85	2	1	8	2

[1] Detection times approximately: A = 0400-0830 hrs; B = 0900-1530; C = 1600-2030; D = 2100-0300

[2] Not enough detections to be used in analysis

[3] No data on transmitter fate
[4] Tracking period continued into breeding season
[5] Tracking discontinued due to crew change and transmitter never recovered (minimum retention days underestimated).
[6] Not included in some analyses due to missing tracking sessions or small number of locations

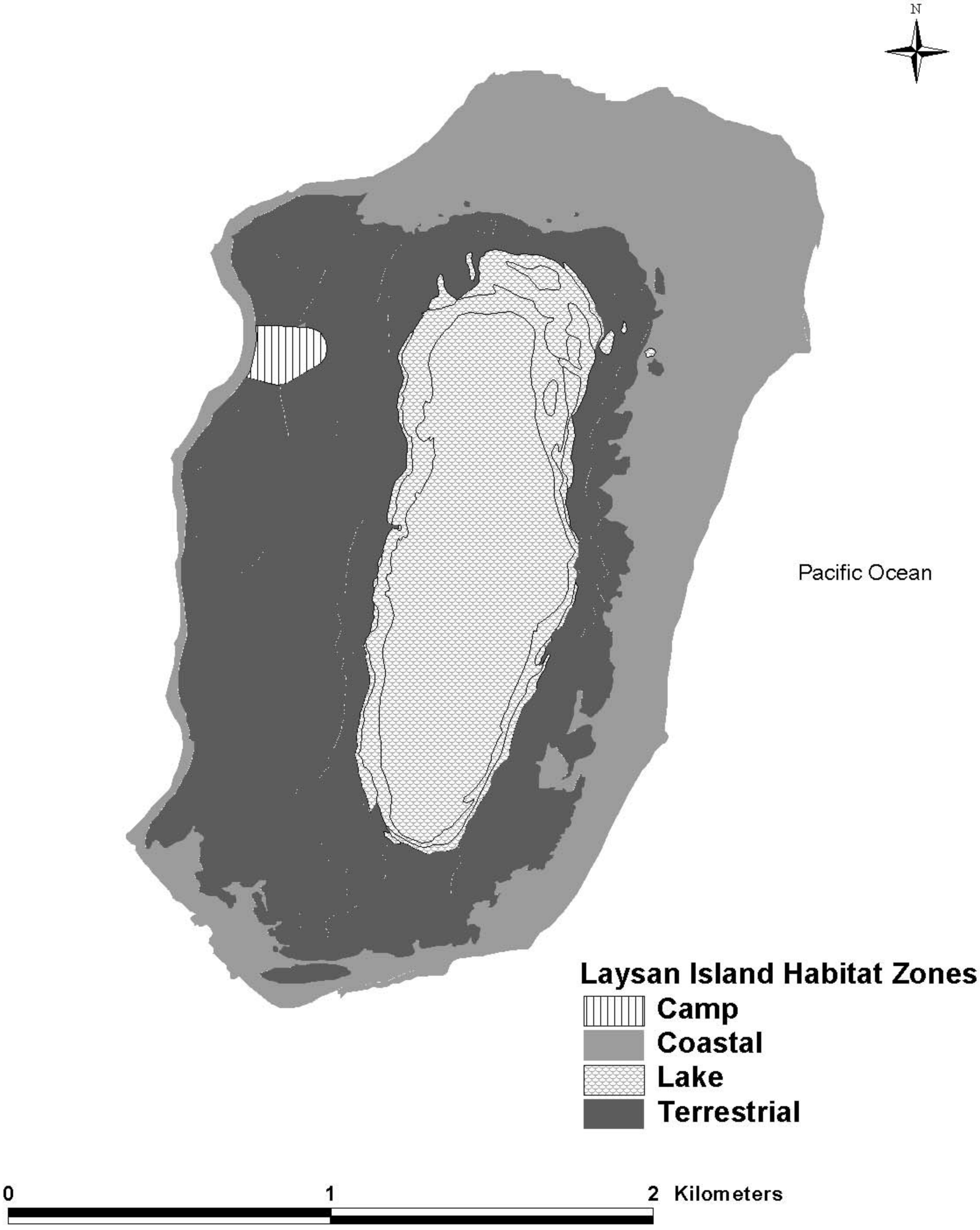

Figure 1. Laysan Island and the habitat zones: camp, coast, lake, and terrestrial

Figure 2. Radio attachment to Laysan teal using surgical glue and tape.

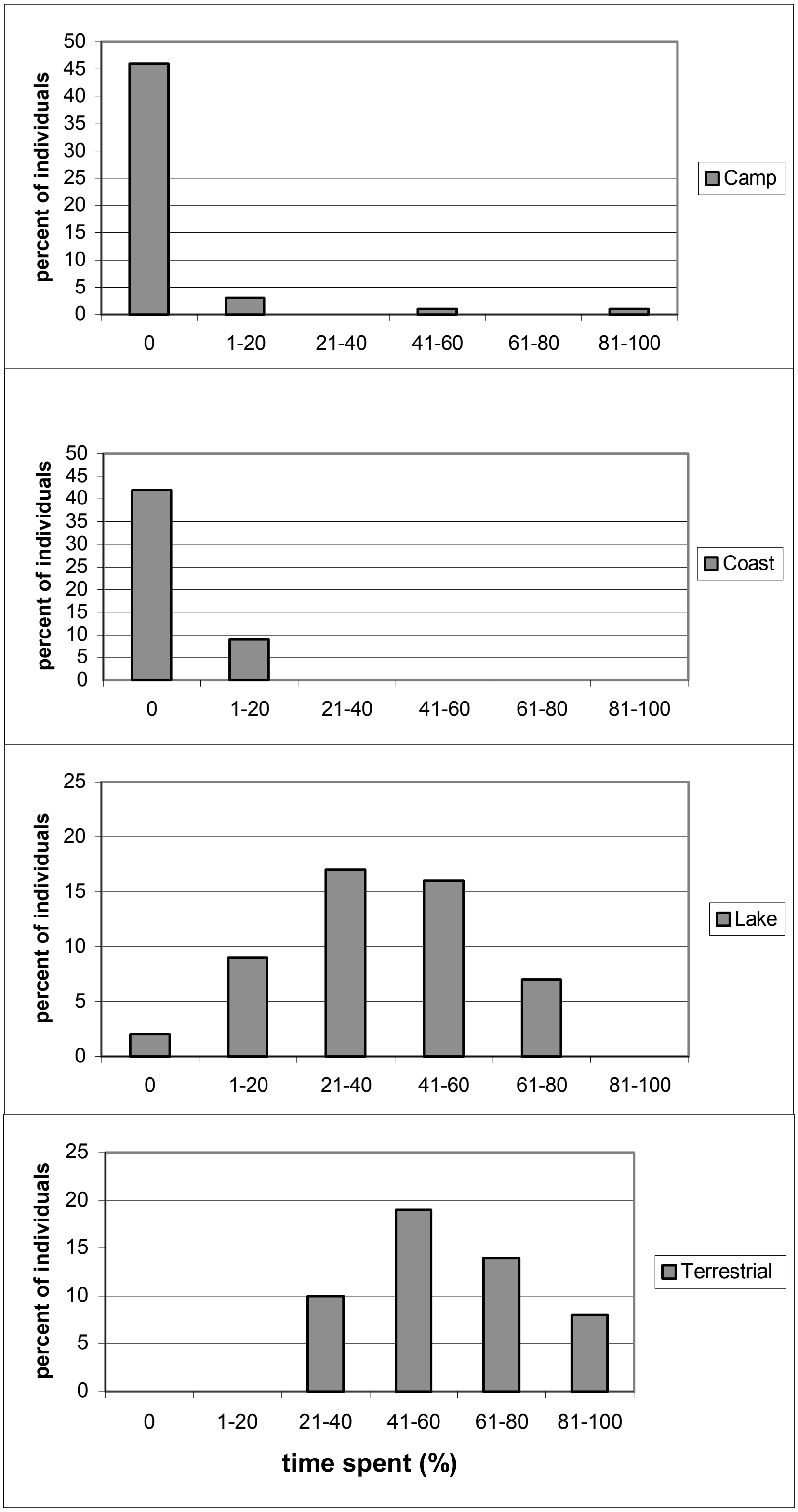

Figure 3. Individual habitat use of Laysan teal 1998-2000 (N=53; 1562).

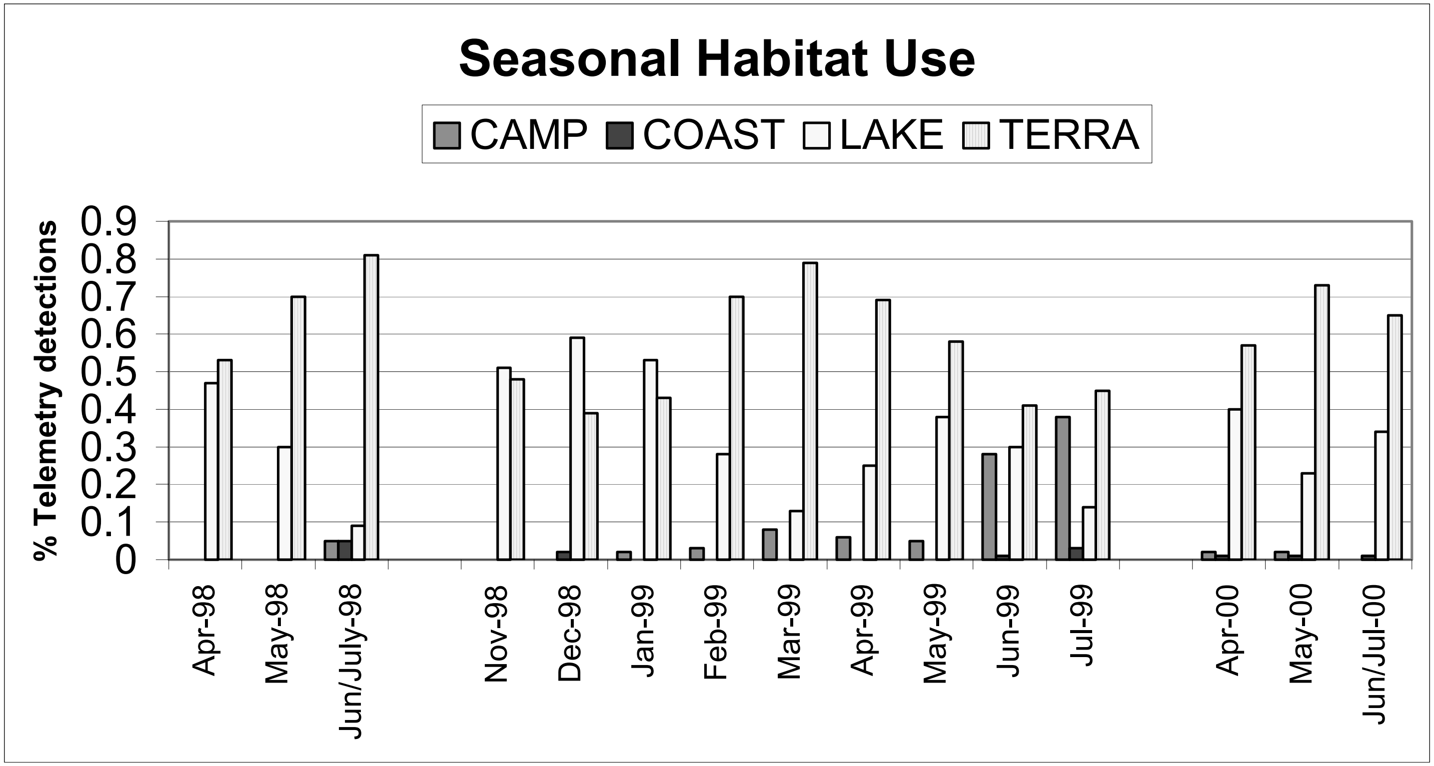

Figure 4. Seasonal habitat use by radio-tagged Laysan teal (n=62) during the the spring and summer of 1998-2000 and the winter of 1998-19999.

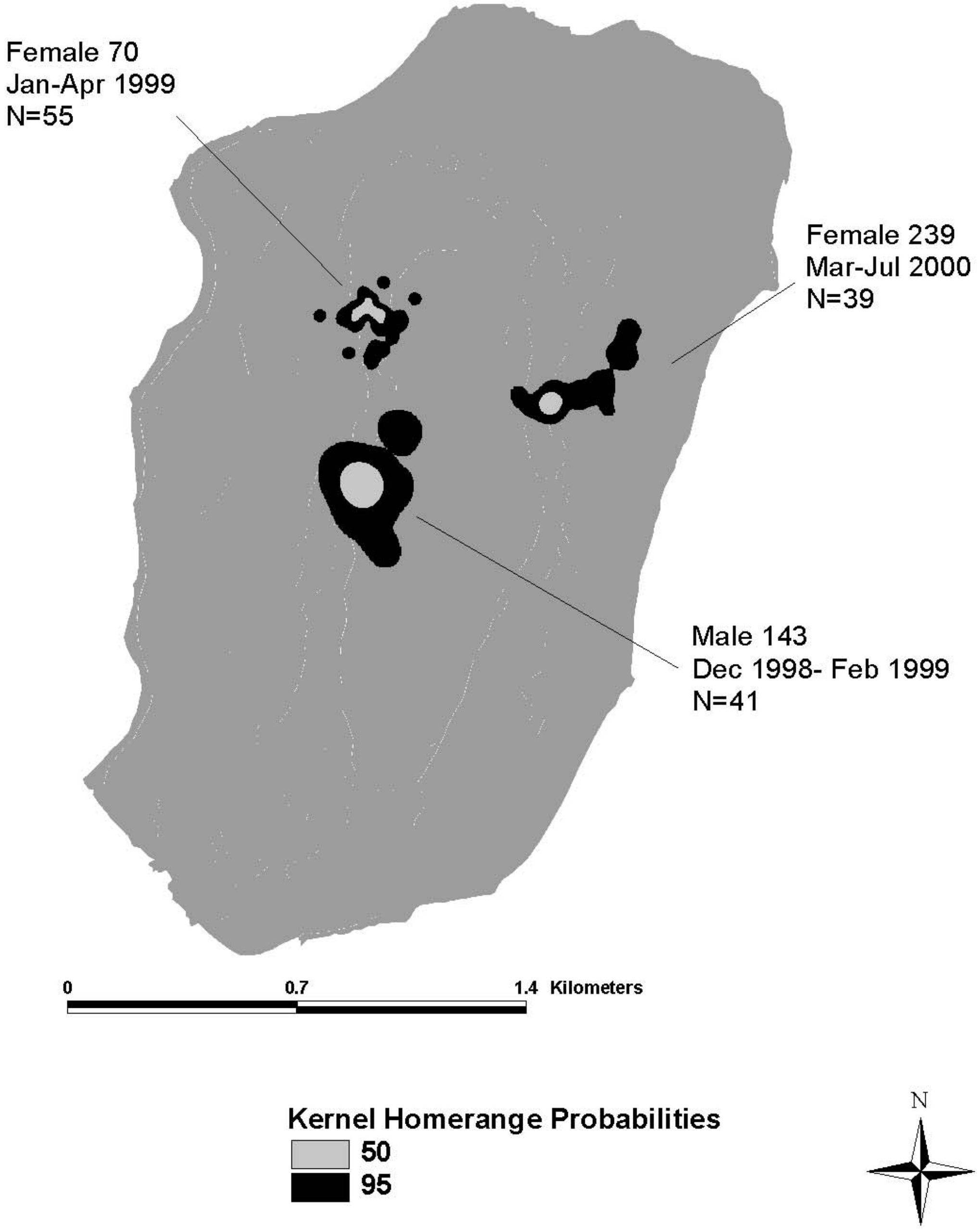

Figure 5. Example of home range and core area estimates (95 and 50% fixed kernel) for three radio tracked Laysan teal (♀ 70, ♀ 239, ♂143, N= locations).

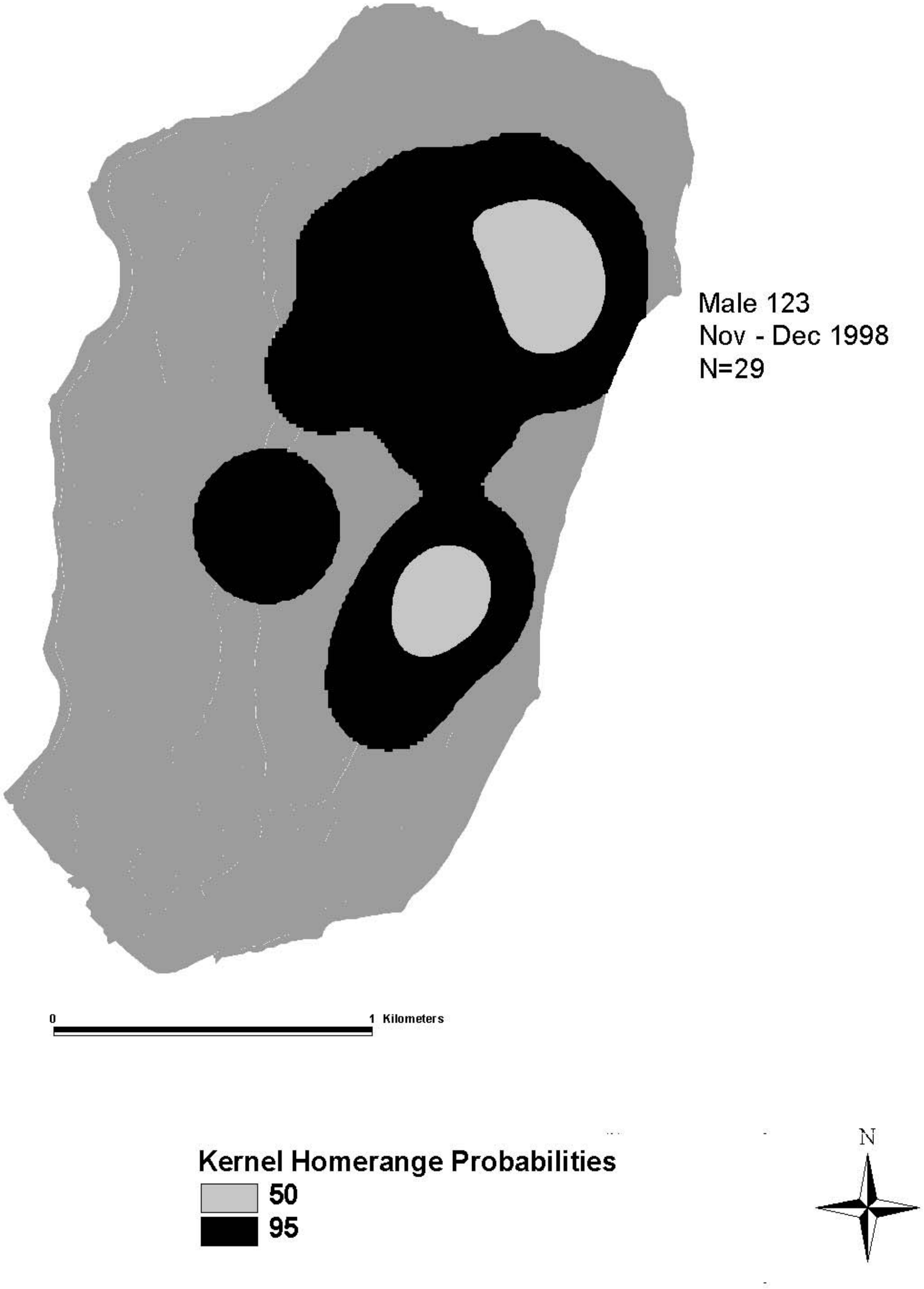

Figure 6. Example of home range and core areas (95 and 50% fixed kernel) of unpaired male 123, radio tracked on Laysan Nov-Dec 1998 (N=29).

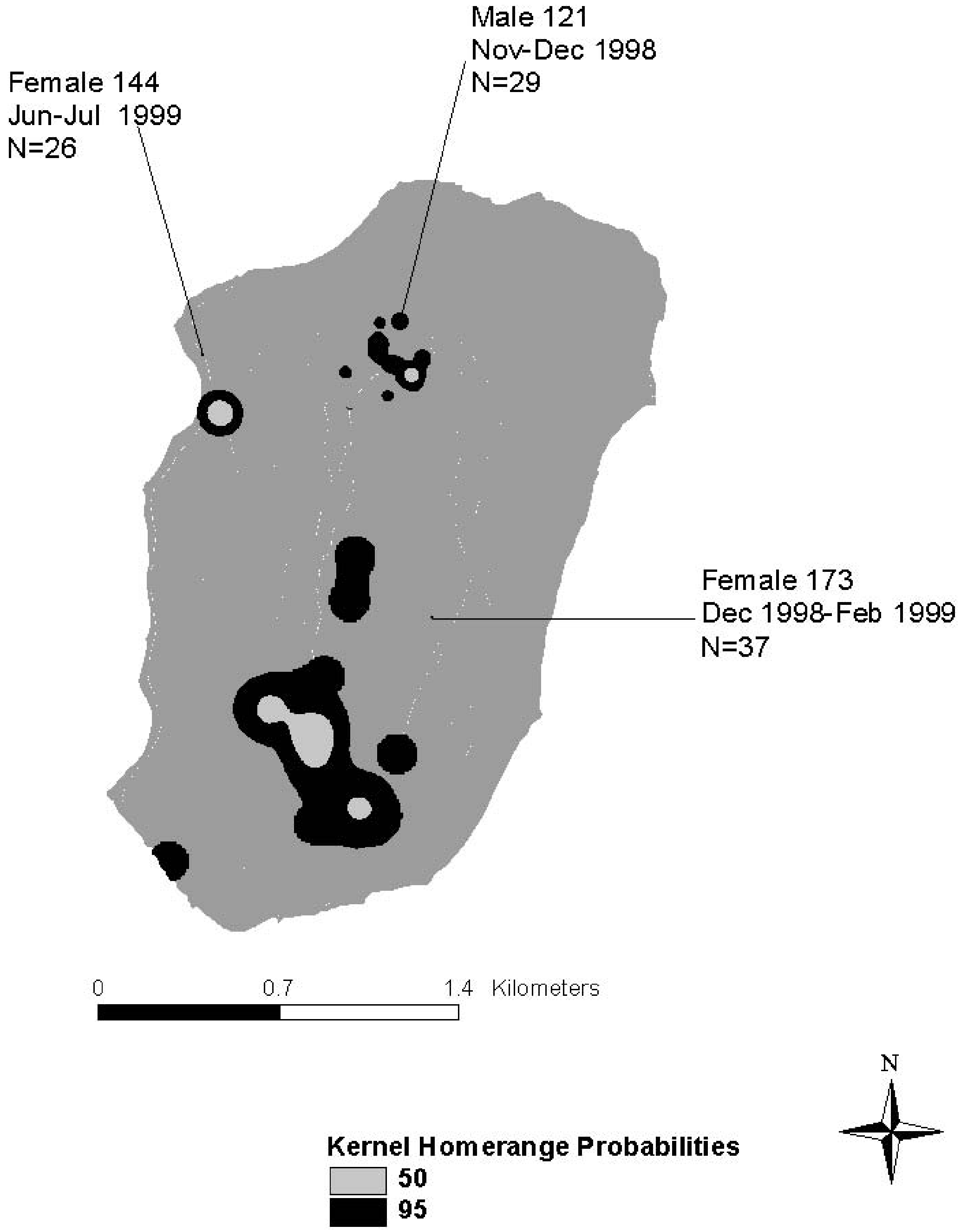

Figure 7. Example of home range and core areas (95 and 50% fixed kernel) of paired female 144, paired male 121, and female 173 radio tracked on Laysan 1998-1999 (N=locations). Female 144 lived and nested in camp, and female 173 was not seen with a mate until February.

RESUMÉ

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EDUCATION

PhD Biology. 2002. Virginia Polytechnic and State University. Blacksburg, VA 24060

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EXPERIENCE

1998-2002	Wildlife Biologist (Research) Student Trainee USGS –Pacific Islands Ecosystems Research Center, HI.
1997-1994	Project Leader- Forest Bird Survey and Rare Bird Search, Hawaii Field Station, HI.
1994-1993	Field Leader - Geothermal Impact Assessment; Wildlife Surveys USFWS, Ecological Services, Hawaii Field Station, HI.
1992	Fish and Wildlife Biologist USFWS, Ecological Services, Honolulu, HI
1991	Endangered Species Research Technician, USFWS, Hawaii Field Station, HI