Laysan Teal *Anas laysanensis* nesting phenology and site characteristics on Laysan Island

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Abstract

Factors influencing breeding initiation of the endangered Laysan Teal *Anas laysanensis* were studied on Laysan Island in the Hawaiian Islands National Wildlife Refuge between 1998 and 2006. Sixty-two radio-tagged adult females were tracked for 30–180 days to locate and describe their nest sites. In addition, the Laysan Teal were surveyed daily during the breeding season, and 331 individually colour-ringed females were marked to identify new broods and timing of incubation initiation. Temperature, rainfall, and abundance of Brine Flies (*Scatella sexnotata*, an important prey) were measured in all years. Females nested on average 213 m (s.e. ± 37 m) from the lake basin primarily in *Eragrostis variablis*, a native bunch grass with > 75% cover. The first observation of nesting in marine debris by Laysan Teal was reported. The initiation of incubation, at the start of the breeding season each year, varied from December to July, and differed significantly between years. Brine Fly abundance, temperature, and rainfall also varied significantly between years. The earlier the Brine Fly abundance peaked, the longer the duration of the breeding season. The length of the breeding season, measured as the number of days between the first and last clutches, varied from 83–192 days (mean 116 ± 14 days). Annual brood production was positively correlated with spring peak abundance of Brine Flies. There was some evidence that it was negatively correlated with the number of adult females in the population. Rainfall, temperature, prey abundance, and the density of other birds on Laysan Island are likely to interact in influencing Laysan Teal's variable nesting phenology and productivity.

Key words: Laysan Teal, habitat selection, incubation initiation, prey abundance, Multivariate El Nino/Southern Oscillation Index.

Prior to recent translocations to Midway Atoll National Wildlife Refuge (USGS 2005), the Laysan Teal, or Duck, *Anas laysanensis* was restricted to a single population on Laysan Island (hereafter Laysan) in the Northwestern Hawaiian Islands for approximately 150 years. Endemic island ducks are globally threatened (Green 1996; Williams 1996), and the Laysan Teal is vulnerable to extinction due to the limited carrying capacity of Laysan and from random catastrophes (USFWS 2004). Reliable information on reproduction is important for the conservation of Laysan Teal. However, Laysan Teal are one of the most difficult birds to monitor in the Northwestern Hawaiian Islands (Sincock & Kridler 1977). Nests and ducklings are difficult to observe because nests are well concealed, breeding females are secretive (Warner 1963; Moulton & Weller 1984), and access to remote Laysan is limited (five days one-way by sea from Honolulu). Traditional waterfowl nest-searching methods (systematic field searches) are inappropriate on Laysan, where it is easy to crush burrows of ground-nesting seabirds, and to expose Laysan Teal eggs to avian egg predators.

Laysan Teal are typically monogamous and nest between March and June (Moulton & Marshall 1996). Ducklings are precocial and leave the nest the day of hatching after a 28–29 day incubation period (Marshall 1989). Females typically provide all parental care until ducklings are 45–75 days old (Moulton & Marshall 1996; M. Reynolds unpubl. data). Adult survival is high (0.88–0.91, s.e. = 0.02; Reynolds & Citta 2007), but duckling survival is much lower 0.10–0.30 (Reynolds & Work 2005). Little is known about factors that influence Laysan Teal breeding behaviour. Brine Flies (Diptera: Ephydiridae: *Scatella sexnotata*) are an important prey to adults and ducklings on Laysan Island (Moulton & Weller 1984; Reynolds *et al.* 2006). This is the first multi-year study of Laysan Teal nesting phenology and nest site selection. Our objectives were to (1) locate and describe nest sites with minimal disturbance, (2) determine if females selected certain vegetation types for nesting, and (3) examine the influence of Brine Fly abundance, rainfall, and temperature on variation in nesting phenology and duckling production.

Study Area

Laysan lies 1,463 km northwest of Honolulu (25°46´N, 171°44´W), and is accessible only by boat (Fig. 1). It is approximately 415 ha in size, and over half of the island is vegetated. Scattered vines (*Ipomoea* spp. and *Sicyos* spp.) and coastal shrubs (*Scaevola sericea* and *Tournefortia argentea*) occur near the beach, while inland vegetation consists of native bunch grasses (*Eragrostis variabilis*), shrubs, vines, and matted vegetation. Sedges (*Cyperus leavigatus*) are scattered around the 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 (Caspers 1981). The lake, with scattered adjacent freshwater and brackish seeps, supports alga and cyano-bacteria growth (*Dunaliella* spp., *Schizothrix* spp.), as well as dense populations of Brine Shrimp (Anostraca: *Artemia franciscana*) and Brine
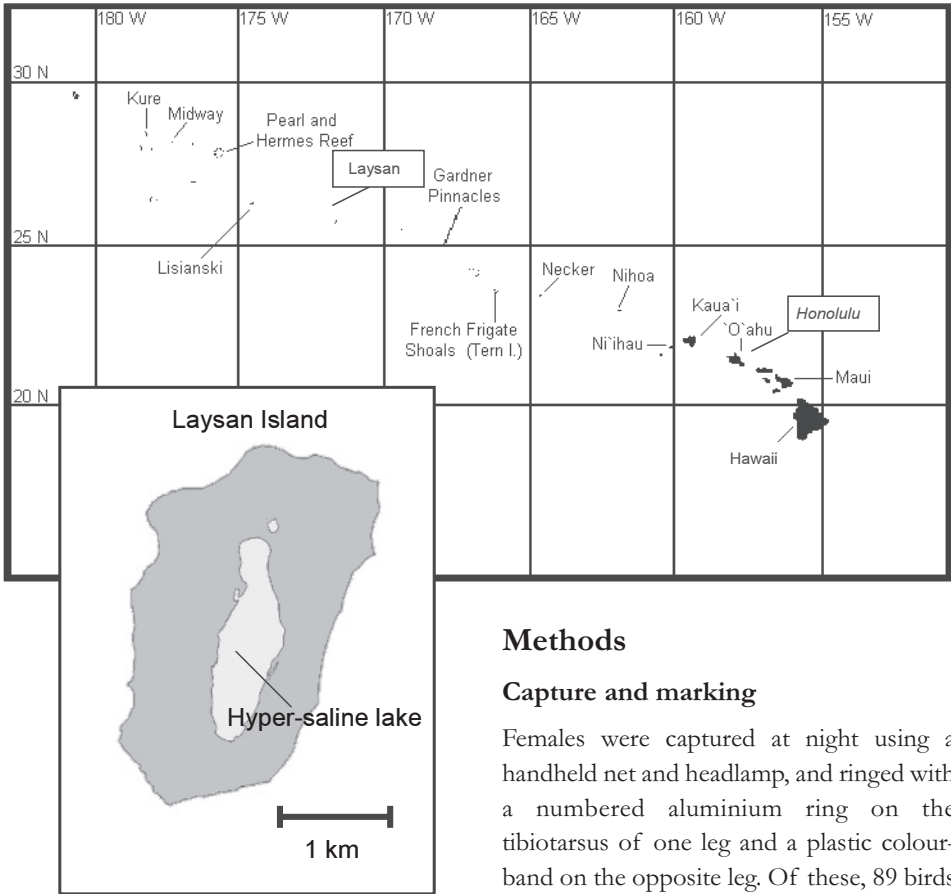
Figure 1. Map of Hawaiian Islands with enlargement of Laysan Island.

Flies (Diptera: Ephydridae: *Scatella sexnotata*) (Caspers 1981; Lenz 1987). The natural history of the island has been described by Ely and Clapp (1973) and by Rauzon (2001). Laysan is part of the Hawaii Islands National Wildlife Refuge (USFWS 1982; NOAA 2001) and the newly designated Northwestern Hawaiian Islands (Papahānaumokuākea) Marine National Monument (NOAA & USFWS 2006).

Methods

Capture and marking

Females were captured at night using a handheld net and headlamp, and ringed with a numbered aluminium ring on the tibiotarsus of one leg and a plastic colour-band on the opposite leg. Of these, 89 birds weighing more than 400 g were fitted with 4.5–9.5 g radio-transmitters (AVM model G3, ATS various models). Transmitters were attached with Tessa™ tape and Skin Bond™ surgical glue (see also Reynolds 2004) or a nylon harness equipped with a weak link of break-away thread.

Nest location and monitoring

Birds were located by radio-telemetry using a three-element handheld antenna for homing (Samuel & Fuller 1996). The habitat at telemetry locations was recorded, including percentage of overhead cover,

horizontal cover, and species composition. Confirmed nest locations were plotted on maps and/or given GPS coordinates (Garmin eTrex Legend™) during April–July 1998, February–July 1999, April–July 2000, April–September 2004, and April–September 2005. Individuals were radio-tracked 2–5 times per week. If birds were in the same location for two consecutive tracking sessions, the presumed nest location was marked with GPS coordinates. In rare cases, observations of females' behaviour led to the discovery of nests without radio-telemetry.

Because Laysan Teal are well concealed when nesting, we report nesting initiation as the start of the incubation, which typically is after egg-laying is complete. The date of the start of incubation was inferred from radio-tracking observations (i.e., radio signals became stationary at night when the birds are typically active, and the females were difficult to find or reluctant to flush from consecutive identical locations), or by back-dating (by 29 days) from the estimated hatch date for newly emergent broods. To prevent disturbance or abandonment of nesting birds and to reduce the risk of exposing nests to avian egg predators, nest measurements (vegetation height, nest cup depth, and interior nest cup diameter) were made only after the normal 29-day incubation period.

Nest site selection

When nests were located, the vegetation within a 2.5 m radius of the nest was classified as *Eragrostis*, vines (*Ipomoea* spp. and/or *Sicyos* spp.), or other (e.g., shrubs, sedges, or mixed vegetation), and observed number of nests in each type of habitat was tallied. The percentage of cover providing horizontal and overhead concealment to nests was estimated visually. Obscurity indices (Robel *et al.* 1970) of *Eragrostis*, vines, and sedges were also recorded using marked "cover" poles on 7 June 1999, with measures taken at 1 m intervals along ten randomly assigned 100 m transects to describe the vegetation physiognomy of these potential nesting habitats (higher index = greater visual obscurity for nesting birds).

The expected number of nests, assuming that nests were located in relation to the total area available (in hectares), was calculated for three vegetation categories. Morin's (1992) data were used to provide estimates of vegetation type availability: 112.6 ha of *Eragrostis*, 50.8 ha of vines, and 23.6 ha of "other" vegetation on Laysan. A chi-squared test was used to determine if the observed and expected numbers of nests differed significantly at $\alpha = 0.05$.

Brood monitoring

During the breeding seasons of 1998–2000 and 2003–2006, broods were checked daily around the lake using a spotting scope (40–60x zoom) and binoculars (10x40; Reynolds & Work 2005). During the rest of the year, and in 2001–2002, surveys were conducted around the lake once per week (Marshall 1992). Females were identified and all ducklings were counted and assigned to an age class based on plumage characteristics or estimated hatch dates (Gollop & Marshall 1954; Moulton & Weller 1984; Marshall 1989). In winter 2006, we used the mid-date of the plumage age

classes reported to estimate early hatch dates. During intensive brood monitoring, duckling aging accuracy is approximately ± 2 days based on a field trial for ducklings of known age (i.e. broods from nesting radio-tagged females). Daily brood surveys provided indices of brood and duckling production (number of unique new broods and the number of ducklings per brood sighted at 1–3 days old) in 1998–2000 and 2003–2006. Because females with failed broods often adopted or stole ducklings, we considered re-nesting to have occurred only if radio-tagged females had a second nest, or if colour-ringed females were sighted with a second brood of 1–3 day old ducklings, i.e., before amalgamations were likely, and after sufficient time for egg-laying and incubation had elapsed.

Environmental variables and prey abundance

Rainfall and temperature were recorded every 24 h at a rain gauge in the field camp on Laysan Island (US Fish & Wildlife Service data). Abundance of adult Brine Flies was sampled bimonthly using interception trapping (Southwood 1978) at four sites around the lake. At each site, eight traps fashioned from 5-gallon bucket lids (660.52 cm^2) were placed 5 m apart on the ground at right angles to the lake edge. Traps were activated between 13:00–16:00 h with several drops of biodegradable soap; after 30 mins, trapped Brine Flies were counted with a handheld counter.

Single factor ANOVA (PROC GLM in SAS 9.1) was used to test for yearly differences in temperature, precipitation and Brine Fly abundance. At the annual scale,

Poisson regression (PROC GENMOD in SAS 9.1) was used to examine the influence of cumulative November–April ("total") precipitation on duckling and brood production each year, with the number of females in the population, which increased over the study period, included as a covariate. Simple linear regression (PROC GLM in SAS 9.1) was used to examine the influence of total precipitation on the first and mean dates of incubation initiation and breeding season length (number of days from first to last nest), and on mean March–June Brine Fly abundance, fall and spring peak Brine Fly abundance, and the dates of those peaks. Regression models (Poisson for brood and duckling production; linear for other variables) were also run with December–February ("winter") precipitation, March–April ("spring") precipitation, mean maximum January temperature, and/or mean maximum March temperature, as predictors of the same suite of dependent variables. To examine the effects of El Nino/Southern Oscillation on reproduction, models with the December–January Multivariate ENSO Index (MEI) and the March–April MEI (Wolters & Timlin 1993; NOAA 2007) were considered.

The number of females was included as a covariate in all brood and duckling production models. We checked and corrected for (by scaling by the deviance) overdispersion and underdispersion in all Poisson regressions. Dependent and independent continuous variables were log transformed as necessary to satisfy assumptions of the statistical models used; counts of broods and ducks were always

square root transformed. The level of statistical significance was set at α = 0.05. Means ± s.e. are reported.

Results

Nest sites

Sixty-two females retained their transmitters for more than 30 days during the nesting season. The number of nests initiated by radio-tagged females varied from zero in 1998 ($n = 7$ radio-tagged females), an El Nino drought year, to 11 in 1999 ($n = 16$ radio-tagged females; Table 1). Of 32 nests sites described, 78% were in *Eragrostis variabilis*, a native bunchgrass, 9% in viney vegetation (*Ipomoea* spp. and *Sicyos* spp.), 6% in sedges (*Cyperus laevigatus*), and 6% in under shrubs (*Scaevola sericea* and *Tournefortia argentea*). One nest located under *Tournefortia* near the coastal high surf line was well concealed in plastic pipe (30 cm diameter, 3 m long), and is the first known account of Laysan Teal nesting in marine debris. Females nested more than expected in *Eragrostis*, and less than expected in vines

Table 1. Summary of Laysan Teal nesting effort and brood production derived from radio-tracking studies and brood monitoring.
NA indicates no data.

Nesting Summaries	1998	1999	2000	2003[1]	2004	2005	2006	1998–2006 Summary
No. radio-tracked females[2]	7	16	10	0	13	16	0	62
No. nest attempts by radio-tagged females[2]	0	11[5]	10[5]	NA	8	7	NA	36[6]
No. nest attempts by untagged females[3]	NA	2	NA	1	NA	NA	NA	3
No. females with broods but no nest located prior to radio detachment	1	0	1	NA	2	0	NA	4
Total no. unique broods	10	79	113	99	55	41	15	412
Approximate broods/female[4]	0.07	0.54	0.70	0.09	0.05	0.03	0.01	0.21 ± 0.11
Total no. new downy ducklings	29	136	189	95	145	82	39	1189

[1] Laysan teal were not radio-tagged in 2003; one nest was discovered during behavioral observations of a marked pair.
[2] Number of females monitored ≥ 30 days during the peak nesting season
[3] Active nesting attempts, as indicated by eggs laid or ducklings observed. Totals do not include nests found incidentally due to exposure or after failure.
[4] Estimated as the number of broods divided by ½ the estimated population size (from Reynolds & Citta 2007).
[5] Excludes a female with nest bowl but no eggs detected.
[6] Excludes the single nest recorded in 2003.

and other available vegetation ($\chi^2_2 = 6.99$, $P < 0.05$). Visual obscurity indices for *Eragrostis,* vines and sedges were 5.2, 3.1, and 4 respectively (higher index = greater visual obscurity).

Mean overhead cover at all nests was $88 \pm 6\%$ ($n = 28$ nests), and horizontal cover was $79 \pm 8\%$ ($n = 18$ nests). Nests in *Eragrostis* typically had greater than average cover; all but two nests had 100% overhead cover (minimum 95%), and all but four had 100% horizontal cover (minimum 80%). Composition of nests in *Eragrostis* included dead *Eragrostis* leaves, stalks, and rootlets, and variable amounts of down. Some active nests had sufficient down to cover the eggs whilst the females were on incubation breaks. Nests in *Ipomoea* and *Sicyos* consisted of dead leaves, stalks and down. Mean height of vegetation surrounding nests was 67 ± 24 cm ($n = 5$ nests). Mean nest diameter and depth were 10.6 ± 1.0 cm ($n = 14$) and 2.8 ± 0.17 cm ($n = 3$), respectively. Most nests (94%) were located in the upland vegetation zone, with a mean distance from the edge of the full lake basin of 213 ± 37 m ($n = 21$).

Nesting phenology

Incubation initiation dates inferred from the sightings of new broods (1–3 day-old ducklings) and radio-tracking varied significantly between years ($F_{3,280} = 22.84$, $P < 0.0001$), ranging from December to July. Dates of the first incubated nests of the season varied by three months, from 25 Dec (for the 2006 breeding season) to 26 March (in 1998 and 2003). The latest onset of incubation recorded each year varied by only three weeks over the study period, ranging from 14 June (in 1999) to 6 July (in 2006).

Incubation initiation sometimes was bimodal, with nesting peaks in early March and again in June in 1999, and nesting peaks in the late March and early May of 2000 (Fig. 2). The onset of incubation was highly synchronous in 2004, but in 2005 there was nearly uniform incubation initiation between mid-April through June. Mean incubation initiation dates ranged from 8 April (s.e. $\pm$ 19 days) in 2006 to 25 May (s.e. $\pm$ 6 days) in 2004; for all years pooled, overall mean initiation date was 20 April (s.e. $\pm$ 2 days).

In springs when there is less rain ($F_{1,4} = 11.2$, $P = 0.029$), or temperatures are lower ($F_{1,4} = 8.32$, $P = 0.045$), incubation of first nests is initiated significantly later. There was some evidence that the spring peak in Brine Fly abundance was negatively correlated with incubation initiation at the first nest, in that the earlier the spring Brine Fly peak, the later the first clutch was initiated after the spring Brine Fly peak, although results did not reach 95% statistical significance ($R^2 = 0.43$, $F_{1,7} = 5.18$, $P = 0.057$; Fig. 3).

Breeding season length (number of days between first and last nest) ranged from 83 to 192 days (mean = 116 ± 14 days), and was significantly predicted by the fall peak date in Brine Fly abundance ($F_{1,4} = 7.33$, $P = 0.05$; Fig. 4). The earlier the fall peak in Brine Fly abundance, the longer the duration of the breeding season. In separate models, total precipitation ($F_{1,4} = 4.89$, $P = 0.08$) and maximum January temperatures ($F_{1,4} = 8.32$, $P = 0.045$) were positively correlated with the size of the fall Brine Fly peak; the higher the temperatures or greater the rainfall, the greater the magnitude of the peak. The number of ducklings ($F_{1,5} = 0.01$, $P = 0.94$)
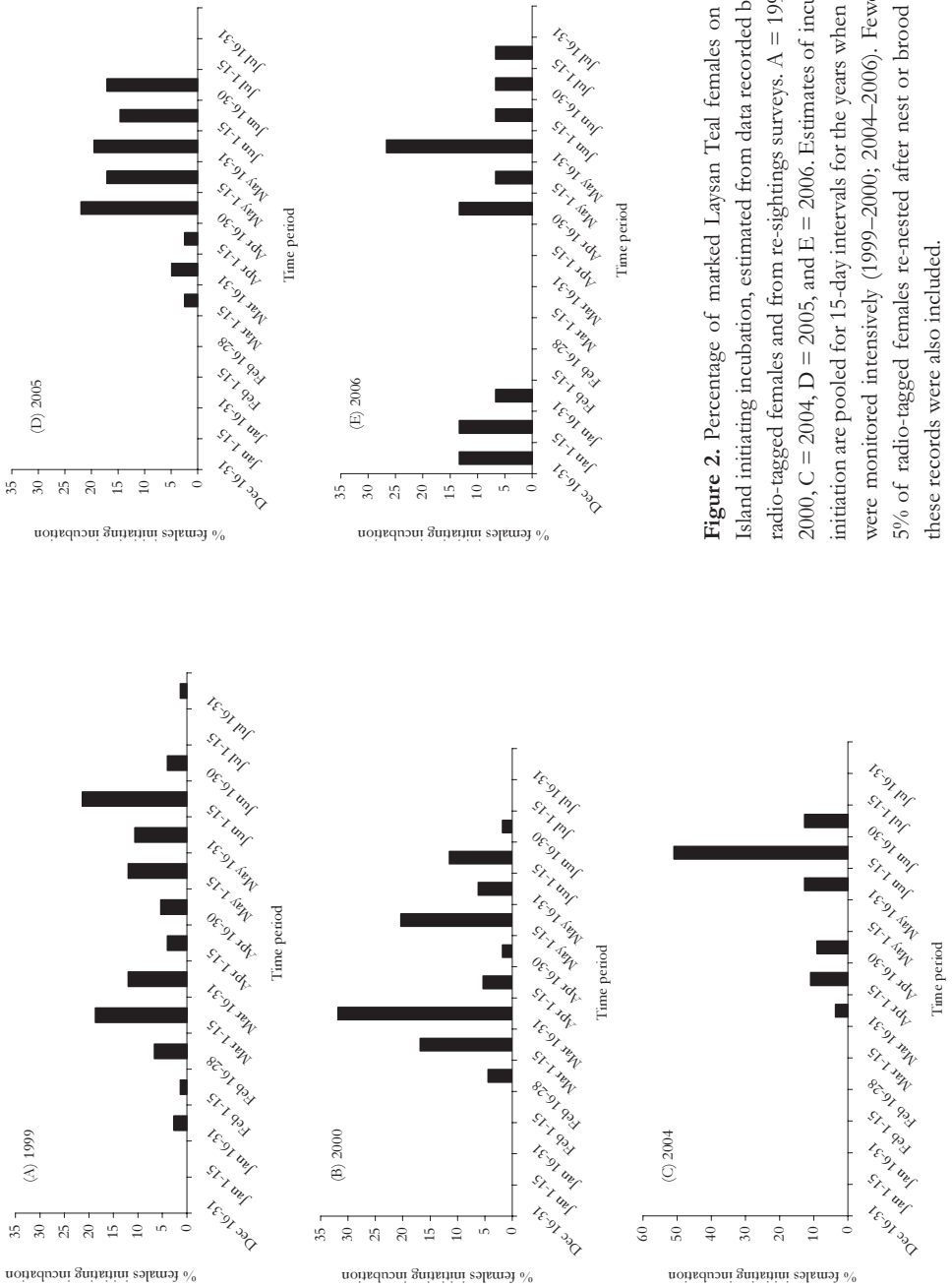
Figure 2. Percentage of marked Laysan Teal females on Laysan Island initiating incubation, estimated from data recorded both for radio-tagged females and from re-sightings surveys. A = 1999, B = 2000, C = 2004, D = 2005, and E = 2006. Estimates of incubation initiation are pooled for 15-day intervals for the years when broods were monitored intensively (1999–2000; 2004–2006). Fewer than 5% of radio-tagged females re-nested after nest or brood failure; these records were also included.
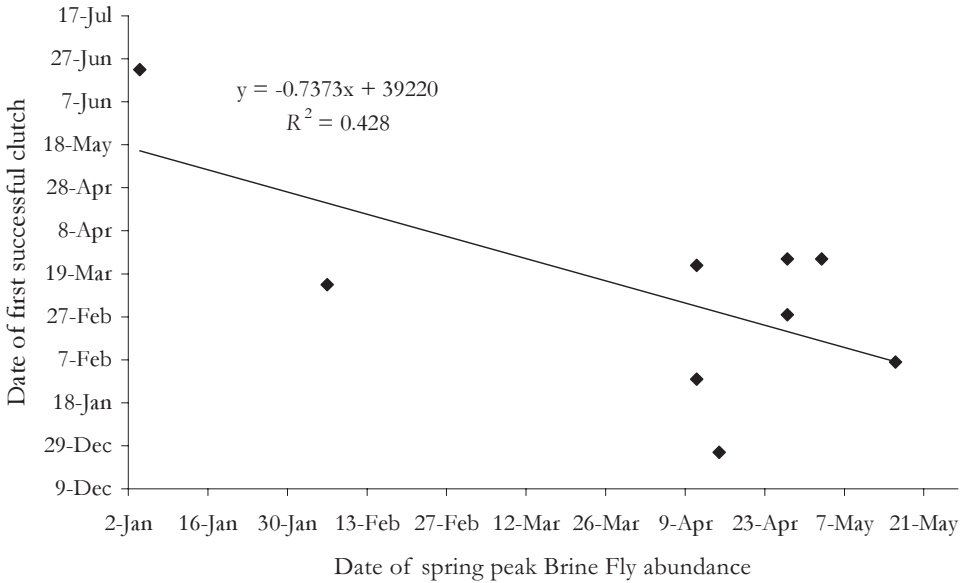
Figure 3. Relationship between the timing of the spring peak in Brine Fly abundance on Laysan and the date of initiation of the first successful Laysan Teal nest in the same year (1998–2006).
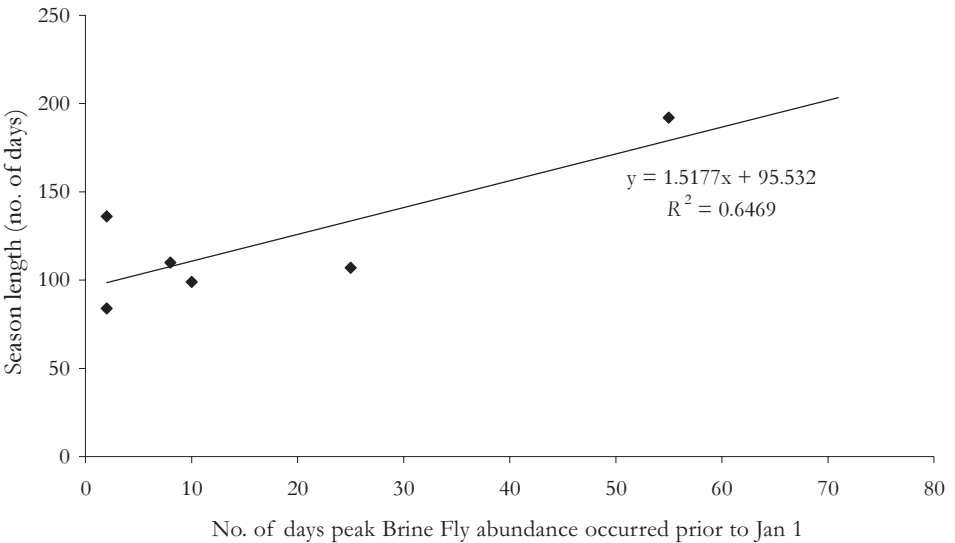
Figure 4. Relationship between the timing of the fall peak in Brine Fly abundance (expressed as number of days prior to Jan 1 that the peak occurred) and the length of the breeding season (no. days between first and last nest) in the subsequent year.

or broods ($F_{1, 5} = 1.27$, $P = 0.31$) produced was not correlated with the length of the breeding season.

Brood and duckling production

The total number of unique broods produced ranged from 10 in 1998 to 113 in 2000 (mean = 59 ± 15 broods; Table 1). Estimated number of females in the population was not a significant predictor of annual brood production when it was the only predictor in the model ($\chi^2_1 = 0.16$, $P = 0.69$), but when it was included as a covariate in other models, it was significantly negatively correlated with brood production in four models, and never significantly positively correlated. Annual brood production was positively correlated with the date of the fall peak in Brine Flies ($\chi^2_1 = 11.58$, $P = 0.0007$), and the magnitude of the spring peak of Brine Flies ($\chi^2_1 = 4.69$, $P = 0.03$; Fig. 5), suggesting that when the fall peak was later and/or there were more flies in the spring peak, more broods were produced.

Annual production of ducklings counted when downy varied from 18–189 ducklings (Table 1), and was positively correlated with annual brood production ($\chi^2_1 = 10.59$, $P = 0.001$). Estimated number of females in the population was not a significant predictor of total downy duckling production when it was the only predictor ($\chi^2_1 = 0.29$, $P = 0.59$), but was a significant negative predictor in two models in which it was used as a covariate. It was never positively correlated with duckling production. There was some evidence, although it did not reach 95% statistical significance, that duckling production was negatively correlated with Dec–Jan MEI ($\chi^2_1 = 3.04$, $P = 0.08$) and with Mar–Apr MEI
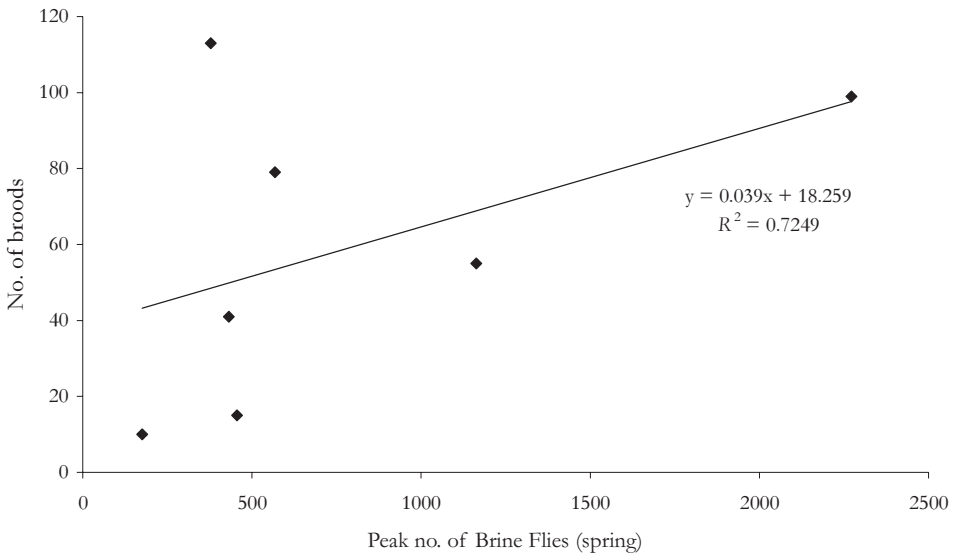

$$y = 0.039x + 18.259$$
$$R^2 = 0.7249$$

Figure 5. Relationship between Laysan Teal brood production and spring peak number of Brine Flies on Laysan (1998–2000 and 2003–2006).

$(\chi^2_1 = 2.85, P = 0.09)$; that is, slightly more ducklings may be produced in years with La Niña conditions. There was also some evidence that more ducklings were produced in years with warmer maximum temperatures in January $(\chi^2_1 = 3.43, P = 0.064)$, and March $(\chi^2_1 = 3.40, P = 0.065)$, although neither result reached statistical significance.

In 2000, a La Niña year, one female successfully fledged her brood, then re-nested and produced a second successful brood. This case is the first documented double-brooding by the species and the only such record for Laysan. Re-nesting after nest failure also is uncommon on Laysan (< 5% of radio-tagged birds; M. Reynolds unpubl. data).

Environmental variables and prey abundance

Mean daily rainfall, maximum temperature and Brine Fly abundance differed significantly among years $(F_{9, 2603} = 20.48, P < 0.0001, F_{11, 2670} = 8.30, P < 0.0001,$ and $F_{8, 175} = 15.06, P < 0.0001,$ respectively) and months $(F_{9, 2603} = 368.4, P < 0.0001, F_{11, 2670} = 3.86, P < 0.0001,$ and $F_{11, 175} = 11.16, P < 0.0001,$ respectively); the year*month interactions were also significant $(F_{74, 2603} = 7.68, P < 0.0001, F_{75, 2670} = 1.94, P < 0.0001,$ and $F_{80, 95} = 15.06, P = 0.0003,$ respectively). Total rainfall between November and April ranged from 12.4 cm (in 1998) to 84.6 cm (in 2002). Mean maximum January temperature ranged from 21.6°C in 1998 to 26.3°C in 2006. Mean Brine Fly abundance ranged from 49 ± 37 flies/site/week in 1998 to 286 ± 36 flies/site/week in 2001, and was typically highest in April (Table 2).

The fall peak number of Brine Flies was positively correlated with winter rainfall $(F_{1, 3} = 58.3, P = 0.005)$ and mean maximum January temperature $(F_{1, 3} = 59.0, P = 0.005)$, and their interaction $(F_{1, 3} = 57.3, P = 0.005)$. The date of the spring peak also was positively correlated with mean maximum January temperature $(F_{1, 5} = 7.75, P = 0.04)$, but negatively correlated with winter rainfall $(F_{1, 5} = 18.84, P = 0.007)$, in the model with both predictors.

Discussion

Laysan Teal exhibited little variation in nest site selection, but highly variable nesting phenology. *Eragrostis variabilis* was disproportionately selected for nesting compared to other vegetation types. *Eragrostis* habitat provides good visual obscurity, does not experience seasonal dieback, and provides structural protection from trampling by Laysan Albatrosses (*Phoebastria immutabilis*) which are seasonally abundant on the island. It may also obscure eggs from avian nest predators such as Ruddy Turnstones (*Arenaria interpres*), Bristle-thighed Curlews (*Numenius tahitiensis*), and Laysan Finches (*Telespiza cantans*; Moulton & Marshall 1996). Therefore, this native bunch grass is being intensively propagated and out-planted as nesting habitat for translocated Laysan Teal on Midway Atoll NWR (J. Klavitter, USFWS Refuge Biologist, pers. comm.).

Incubation initiation dates and synchrony within the breeding season varied greatly on Laysan. The onset of nesting and duration of the breeding season were both correlated with Brine Fly peak densities, suggesting

Table 2. Annual and seasonal variation in rainfall, temperature, Multivariate ENSO Index (MEI), and Brine Fly abundance on Laysan Island, 1998–2006.

Variable	1998	1999	2000	2001	2002	2003	2004	2005	2006
Nov–Apr rain (cm)	12.8	56.4	47.8	78.8	84.6	29.5	29.7	42.1	49.8
Mean maximum Jan temp (°C)	21.6	25.9	NA	25.9	25.3	23.4	24.6	22.8	26.3
Mean maximum Mar temp (°C)	25.0	24.6	26.9	26.1	24.7	25.3	25.2	23.9	25.0
Dec–Jan MEI	2.4	–1.0	–1.1	–0.5	0.0	1.2	0.3	0.3	–0.4
Mar–Apr MEI	2.6	–0.9	–0.3	–0.1	0.4	0.4	0.3	0.6	–0.6
Spring peak no. of flies	175.6	567.9	378.1	290.0	644.6	2,272.0	1,163.0	431.3	455.6
Mean no. of flies in spring	77.4	67.6	43.0	21.8	9.6	15.9	21.9	25.8	34.2
Fall peak no. of flies	NA	79.9	137.0	626.6	420.7	22.8	82.0	582.8	435.0

that Laysan Teal were opportunistic in timing their breeding in response to favourable conditions. There also was some evidence that Laysan Teal reproduction was influenced by annual variation in rainfall, temperature, MEI, and Brine Fly abundance. The magnitude of the spring Brine Fly peak positively affected brood production. In this study, there were no statistically significant correlations between weather and productivity, but there was some evidence that there were more ducklings in years with La Niña conditions and warmer temperatures, and the phenology of nesting was correlated with some weather variables. Nesting was later in years with high spring rainfall and/or temperatures; perhaps females nested later to take advantage of foraging opportunities during the spring peak of Brine Fly abundance. Winter rainfall and temperatures influenced the timing and magnitude of

peaks in Brine Fly abundance, which in turn influenced nesting phenology. Longer breeding seasons did not lead to higher brood production during the years of this study.

Prey abundance and environmental variables can influence duck reproductive effort in other systems (e.g., Gardarsson & Einarsson 1994; Dzus & Clark 1997; Gardarsson & Einarsson 2004; Gardarsson 2006). El Niño Southern Oscillation (ENSO) events can disrupt normal rainfall patterns, causing droughts in some years. ENSO events in 1987 and 1992 resulted in complete Laysan Teal reproductive failure (Moulton & Marshall 1996).

Although we did not have large enough sample sizes to consider more complex models, we suspect that interactions between density dependence, interspecific interactions, weather and the resulting changes in food abundance may influence

differences in annual reproduction. In such an unpredictable environment as Laysan's, an individual's previous year's reproductive success and the total population density may also affect body condition for the onset of laying and incubation. Interestingly, there was some evidence that the size of the female population was negatively correlated with brood and duckling population, when other environmental factors were considered. Density dependence has been suggested for this species (Moulton and Marshall 1996), and might interact with environmental conditions to influence reproductive effort. In a future paper, we plan to compare nest success and other reproductive parameters between the Laysan Teal on Laysan and the re-introduced population on the Midway Atoll NWR.

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