Circadian habitat use, home range and behaviour of Laysan Teal *Anas laysanensis*

MICHELLE H. REYNOLDS[1], JEFF S. HATFIELD[2],
LISA H. CRAMPTON[3,4], MARK S. VEKASY[1,5] & ERIK TWEED[3,6]

[1]U.S. Geological Survey, Kilauea Field Station, Pacific Island Ecosystems Research Center,
Hawaii National Park, Hawaii 96718, USA.
E-mail: michelle_reynolds@usgs.gov
[2]U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road,
Laurel, Maryland 20708, USA.
[3]Hawaii Cooperative Studies Unit (PACRC, UH Hilo), Pacific Island Ecosystems
Research Center, Hawaii National Park, Hawaii 96718, USA.
[4]Current address: Kauai Forest Birds Recovery Project, PO Box 458, Waimea,
Hawaii 96796, USA.
[5]Current address: Dept. of Fish and Wildlife, 600 Capitol Way N, Olympia,
Washington 98501, USA.
[6]Current address: 3918 SE Boise St., Portland, Oregon 97202, USA.

Abstract

The Laysan Teal *Anas laysanensis* is a non-migratory duck that survives as a single relict population on a small remote Pacific atoll, Laysan Island (4 km^2). The species suffered range contraction and isolation after mammalian predator introductions to the Hawaiian archipelago. An understanding of spatio-temporal behaviour on Laysan Island may help guide conservation priorities such as habitat restoration and reintroductions on additional islands. This study therefore analysed factors influencing spatio-temporal variation in Laysan Teal's habitat use. Diurnal, nocturnal and crepuscular (*i.e.* twilight) behaviour and home range utilisation (95% and 50% fixed kernels) of nesting and non-breeding adults on Laysan Island were determined using radio telemetry. Total home range (mean ± s.e.) was 17.69 ± 4.28 ha with core area use of 2.57 ± 0.54 ha ($n = 27$). There was little overlap between core diurnal and nocturnal activity centres. Total home range of non-breeders was larger than that of nesters, and crepuscular movements were larger than diurnal and nocturnal movements. Time of day influenced the Laysan Teal's use of vegetation type and behaviours. Differences in behaviour, prey abundance, and rainfall were observed between years of this study, and Laysan Teal were detected spending more time foraging at night in 2004 during drier environmental conditions compared to 2005, a wet year. Since Laysan Teal do not migrate or disperse from Laysan Island, significant inter-annual differences in rainfall and food abundance are likely to strongly influence resource use and behaviour within their very limited geographic range. These results emphasise that habitat management for threatened species, especially those with restricted mobility and small ranges, should accommodate their circadian use of resources, and inter-annual environmental variability.

Key words: compositional analysis, kernel home range estimators, Laysan Teal, Laysan Island, radio telemetry.

Successful endangered species recovery is more likely when based on detailed knowledge of habitat requirements (Orians & Soule 2001). Identifying spatio-temporal variation in habitat use and behaviour is important for understanding how animals meet their needs to survive, reproduce (Gross 2005; Beier *et al.* 2006), and respond to environmental change (Lewis *et al.* 2005). However, researchers may ignore seasonal, circadian, and individual differences in space use. For example, although many waterbirds forage nocturnally (Guillemain *et al.* 2002; Herring & Collazo 2005), this behaviour is rarely studied, leading to an incomplete picture of species' requirements or inappropriate management recommendations (Gross 2005; Beier *et al.* 2006). Understanding variation in habitat use is especially important for managing wildlife refuges for animals with limited mobility, where a species must meet all of its life history requirements within a restricted ecosystem.

The Laysan Teal *Anas laysanensis*, endemic to the Hawaiian archipelago, is listed as Critically Endangered (BirdLife International 2009). This non-migratory dabbling duck vanished from the main Hawaiian Islands during Polynesian colonisation and mammalian predator introductions 1000 to 1200 years ago (Cooper *et al.* 1996; Burney *et al.* 2001), and from Lisianski Island (26°04'N, 173°08'W) about 150 years ago (Olson & Ziegler 1995). Today, Laysan Island (25°46'N, 171°44'W) lacks non-native terrestrial mammals, but the size of the remnant Laysan Teal population has fluctuated between 20 and 688 adult birds in the last century (U.S. Fish and Wildlife Service (USFWS) 2009) and, since 1991, between 316 and 636 birds 95% of the time (Seavy *et al.* 2009). Like other small, isolated populations, it is highly vulnerable to stochastic events that can lead to extinction (Shaffer 1981; Seavy *et al.* 2009). Since natural dispersal from Laysan Island does not occur, wild translocation to additional islands, after removal of non-native mammalian predators, are components of ecosystem repair recommended to reduce extinction risks to the Laysan Teal (Aldrich 1980; Williams 1996; Reynolds *et al.* 2008; USFWS 2009).

Habitat selection and home range size have been described for a diverse sample of adult Laysan Teal on Laysan Island using 24 h tracking data (Reynolds 2004). These studies indicated circadian, seasonal and individual differences in space use; however, sample sizes and tracking durations were insufficient to estimate home range by time of day or to examine differences associated with reproductive status. Previous and current home range studies on Laysan Island and Midway Atoll observed that gender did not influence home range size (Reynolds 2004; USGS unpubl. data). This study investigated home range size, habitat use and behaviour of Laysan Teal at two temporal scales: circadian and annual. The objectives were to: 1) compare total, diurnal, nocturnal and crepuscular (twilight) home ranges of nesting and non-breeding birds, 2) assess circadian habitat use and behaviour patterns of nesting and non-breeding birds, and 3) examine how prey abundance and precipitation between the two years of the study covaried with space use and foraging. By assessing home range behaviour and habitat use by Laysan Teal, this study sought to guide habitat management and vegetation restoration, and thus to improve chances of population establishment at reintroduction sites.

Methods

Study area

Laysan Island (hereafter Laysan) is in the central Pacific Ocean and part of the Papahänaumokuäkea (Northwestern Hawaiian Islands) Marine National Monument under the jurisdiction of the National Oceanic and Atmospheric Administration (NOAA) and U.S. Fish and Wildlife Service (USFWS) (NOAA & USFWS 2006). Laysan is uninhabited and lies 1,463 km northwest of Honolulu, and is currently accessible only by a five-day boat journey (Fig. 1). It is approximately 415 ha in size, and most of the island is vegetated. Scattered vines *Ipomoea* sp. and coastal shrubs *Scaevola sericea* and *Tournifortia argentea* occur near the beach, while inland vegetation consists of a native lovegrass *Eragrostis variabilis*, interior shrubs *Pluchea indica*, *S. sericea* and *Chenopodium oahuensis*, vines *Ipomoea* sp. and *Sicyos* sp., and matted vegetation *Sesuvium* sp. and *Heliotrope* sp.. Sedges *Cyperus leavigatus* are scattered around the hyper-saline lake and adjacent mudflats near the centre of the island (Caspers 1981). The lake is surrounded by freshwater and brackish seeps. Ely and Clapp (1973) and Rauzon (2001) describe the natural history of the island in further detail.

Capture and tracking of Laysan Teal

Laysan Teal were captured from April–September 2004 and from March–August 2005 using a flexible hand-held net or noose carpet (Bub 1991; Reynolds *et al.* 2007). Teal were fitted with 6–12 g radio transmitters appropriate for their body weight (≤ 3% of body mass; transmitter ATS models 1080 and 1240 [Advanced Telemetry Systems, Isanti, Montana, USA] and AVM models G3-V1 [AVM Instrument, Colfax, California, USA]), focusing on adult females to locate nests (Reynolds *et al.* 2007) and to identify family groups and non-siblings as translocation candidates (USGS 2005). Transmitters were attached to the skin near the proximal end of the synsacrum with surgical glue (Raim 1978) or as a backpack with weak link harnesses (Sirtrack Ltd, Havelock, New Zealand). Radio telemetry locations were determined by homing (Samuel & Fuller 1996) using hand-held antennae (three-element Yagi) and receivers (Telonics, Mesa, Arizona, USA). A global positioning system (GPS) was used to record telemetry locations or locations were

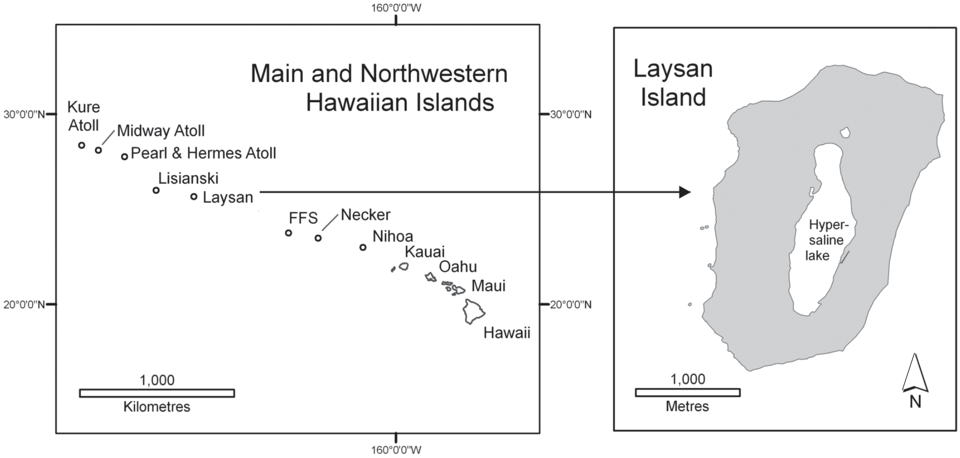

Figure 1. Laysan Island lies 1,463 km northwest of Honolulu (25°46'N, 171°44'W) and contains an interior hyper-saline lake.

plotted directly on a map and coordinates obtained later using the programme MapSource™ (Garmin International, Olathe, KS). GPS accuracy was reported in meters; if the distance between the tracker and the bird exceeded the GPS error, that additional distance was added to provide a better estimate of location accuracy. Locations with > 50 m accuracy were excluded from the analyses. Transmitters which had not become detached from the teals by the end of the study were removed from the birds.

Radio tracking was divided into three periods: diurnal (09:00–15:30 h), nocturnal (21:00–03:00 h), and crepuscular (two hours before or after sunrise and sunset). One location per individual per period or per day was collected to reduce autocorrelation. If a signal location was stationary after two tracking sessions, the presence of birds was visually confirmed to determine nesting, transmitter detachment, or mortality. Time of detection, detection type (signal received and visually confirmed), observed behaviour on first sighting, habitat use, and geographic habitat zone were also recorded (Reynolds 2004). For analyses, eight vegetation types were defined: *Eragrostis*, vine, shrub (> 80% *Eragrostis*, vines or shrubs respectively), mixed *Eragrostis*-vine (21%–80% vine or *Eragrostis*, with the other group dominating the remaining vegetation), mixed shrub (21%–80% shrubs), mixed low vegetation (≤ 20% shrubs, and > 20% grasses and/or terrestrial sedges and/or matted vegetation), wetland (in the lake zone and containing ≥ 50% sedges or matted vegetation), and mudflats or water (in the lake zone and cover = 0%). Vegetation cover, or the combined density of horizontal and overhead vegetation, measured in a 2.5 m radius circle around the located bird, was defined as full (> 95%), heavy (71%–94%), moderate (31%–70%), or sparse (≤ 30%). Behaviours were grouped as follows: "under cover" (subject concealed in vegetation, activity not known), "alert" (flushed, frozen on the spot, looking up, vigilant), "active" (vocal, social, locomotory, self maintenance activities), "loaf" (resting, sleeping, lying, head tucked), "search-forage" (searching, drinking or actively taking food), and "incubate" (incubating eggs).

Home range and statistical analysis

Fixed kernel home range estimators were used to describe the area utilised and probability of use by radio-tagged individuals (Millspaugh *et al.* 1998). Estimates of home range were calculated with the Animal Movements Extension for ArcView 3.2 (Hooge & Eichenlaub 1997). Least square cross validation was applied to select smoothing parameters with minimum estimated error for home range estimates (Seaman *et al.* 1999). Utilisation distributions were applied to describe an animal's probability of occurrence within its home range; areas of concentrated use or core areas were represented by 50% utilisation kernels, while 95% utilisation kernels were taken to describe the total home range. The initial minimum sample size requirements per individual for home range analyses were based on a previous study (Reynolds 2004). Next the Pearson's correlation coefficients were calculated and tested for correlations between total home range size, number of locations, and tracking duration of total home ranges. Rather than exclude birds from this study, if individuals fell short of the minimum sample size of ≥ 25 locations (*i.e.* only 21–24 locations were recorded), one to four randomly chosen capture or resighting locations collected for that individual during the study period were included. Total, diurnal, nocturnal, and crepuscular home ranges were estimated for Laysan Teal with ≥ 25 locations per time period to examine circadian range shifts. The percent overlap of home range kernels was calculated with the spatial overlay tool in ArcGIS 9.3 using the formula: $[\text{Area}_{\text{intersect } 1, 2} / (\text{Area}_1 + \text{Area}_2 - \text{Area}_{\text{intersect } 1, 2})] * 100$ (Millspaugh *et al.* 2004). This measure is highly correlated with other measures of area overlap and is therefore expected to perform well as an index of home range overlap (Millspaugh *et al.* 2004).

In this study the effects of reproductive status (whether or not a duck nested that year), year, and their interactions on log-transformed home range size (95% and 50% kernels), and maximum distance travelled (*i.e.* the maximum distance between any two locations for that individual) were analysed with a repeated measures analysis of variance (ANOVA) with PROC MIXED (SAS Institute 2003) using individual ducks as the random subject effect. Additionally, a repeated measures ANOVA with individual birds as the random subject was used to examine effects of time of day and reproductive status on home range size (95% and 50% kernels) and maximum distances between tracking observations. Here the effect of year was not controlled for when relating home range size to reproductive status since only two of the tracked birds bred in 2004.

The proportion of locations were calculated in each habitat type or cover category during each time period. The proportion of each behaviour in each time period and each behaviour in each habitat type (small sample sizes precluded a full multi-factor analysis) was then determined. These proportions were used to construct a time budget and for compositional analysis with multivariate analysis of variance (MANOVA) (Aebischer *et al.* 1993) in PROC GLM (SAS Institute 2003) to assess whether Laysan Teal's habitat use or behaviour differed among the time periods. The effects of year and reproductive status were controlled for in all MANOVAs. Log ratios were calculated for compositional analysis and, as recommended by Aebischer *et al.* (1993), habitat use or behaviour log-ratio values of 0.00 were replaced by 0.01. The "*Eragrostis*" vegetation type, "full" cover category, and "under cover" behaviour were used as reference groups. All birds with ≥ 10 observations were included, but no incubation records for breeding females were included, so that multiple nest records from the same location (*i.e.* incubation) did not dominate habitat use or behaviour patterns in the analyses.

Here $\alpha = 0.05$ is reported as the level of significance, standard error (s.e.) is given in all statistical tests, and the level of significance for Tukey's multiple comparisons is adjusted in *post hoc* tests. Type III sums of square results are reported in ANOVAs and Wilk's Λ statistic in MANOVAs. Because the MANOVAs involved repeated measurements of individuals over the three time periods (diurnal, nocturnal, crepuscular), individual birds, nested within year and nesting status, were used as the error term for testing years, nesting status, and their interaction (*i.e.* MANOVAs are adjusted for the repeated measures). In addition, the exact option in PROC GLM was used to obtain exact P values for Wilks' Λ rather than approximations based on F tests. The mean log ratios calculated from the MANOVAs are least square means computed from the same habitat use and behaviour data used for the MANOVAs. Interpretation of the mean log ratio is explained in Aebischer *et al.* (1993). For example, if the mean log ratio is > 0 for a particular comparison among habitats, it implies that particular habitat was used more than expected, relative to the reference habitat. Conversely, if the mean log ratio is < 0 for a particular comparison among habitats, it implies that particular habitat was used less than expected, relative to the reference habitat. This also implies that the reference habitat was the most used habitat type (Aebischer *et al.* 1993).

Brine Fly and rainfall sampling

The annual difference in food and rainfall were examined as factors likely to influence habitat use and reproduction of Laysan Teal (Reynolds 2002, 2004; Reynolds *et al.* 2007). Wetland adult dipterans (Brine Flies *Scatella sexnotata*), an important food source for Laysan Teal, were sampled using interception trapping (Southwood 1978; Reynolds *et al.* 2007) at four sites around the lake, twice monthly between 13:30–17:30 h. At each site, eight water traps fashioned from 5-gallon bucket lids (660.52 cm^2) were placed 5 m apart on the ground along a transect radiating from the lake edge and activated with several drops of biodegradable soap. After 30 min, Brine Flies were counted at the traps. Precipitation was recorded daily at 08:00 h on Laysan using a cylindrical rain gauge (USFWS data).

Results

Transmitters were attached to 33 Laysan Teal during this study. Due to transmitter loss or insufficient sample sizes, habitat use and behaviour data from 32 of the radio-tagged birds were included in MANOVA analyses. The movements of 25 birds with 1,448 telemetry, capture, and resighting locations were analysed for home range estimates. Tracking durations included in home range analyses were from 57–119 days. Twelve of the radio-tracked females nested during this study. Two females were tracked in 2004 and 2005; both females nested in 2004, but not 2005; separate home ranges were calculated for each year. Non-breeders included four second-year birds (SY, typically pre-breeders), two unpaired females, and two unpaired males.

Home ranges

Twenty seven home ranges (25 unique birds, two birds were measured both in 2004 and 2005) had sample sizes sufficient (≥ 25 locations per time period) for circadian home range analysis (Table 1). After omitting birds with < 25 locations, no correlation was observed between total home range size and tracking duration (r^2_{25} = 0.09, n.s.) nor the number of telemetry locations (r^2_{25} = 0.32, n.s.). GPS location error (mean ± s.e.) was 5.14 ± 0.2 m (n = 729, range = 3–11 m). Estimates of total home range averaged 11.11 ± 2.80 ha in 2004 (n = 10) and 21.56 ± 6.49 ha in 2005 (n = 17). Core areas of use (*i.e.* 50% kernel) averaged 1.57 ± 0.32 ha and 3.16 ± 0.81 ha in 2004 and 2005, respectively.

Two individuals that nested in 2004 but not 2005 had larger total home ranges (4 ha and 8 ha larger) in their non-breeding year. Home range fidelity between years (measured as kernel overlap) was 59% (17% core) for bird No. 420, and 50% (0% core) for bird No. 422. On average, non-breeders had significantly larger mean total home ranges (95% kernel; 22.66 ± 6.57 ha; $P < 0.05$; repeated measures ANOVA) than nesters (11.47 ± 4.73 ha; Table 1). The size of core areas (50% kernel) did not differ between nesters and non-breeders, or between years (Table 1). There were no significant size differences in total home range or core areas in relation to time period and breeding status (Table 1). Circadian core area overlap varied from 0–74% (n =10), with most birds' area overlap occurring between diurnal and nocturnal (50% kernels) time periods at < 30% (Fig. 2a, b, c).

Movements

Distances between any two tracking locations recorded for an individual bird ranged from 0–1,492 m. The mean distance between telemetry locations was 160 ± 15.5 m (n = 27). Mean maximum distance between locations per individual was 749 ± 65 m (range = 89–1,492 m) and differed according to breeding status and year (Table 1), with nesters in 2004 travelling significantly less than non-breeders in 2004 or both groups in 2005 (Tukey's tests, $P < 0.02$). Maximum distances also differed among time periods (Table 1, $P < 0.05$), with the trend being that crepuscular movements were largest, followed by diurnal, and then nocturnal.

Table 1. Summary statistics (F values$_{df}$ and P values) from the repeated measures analysis of variance (ANOVA) of the effect of reproductive status with year and time period on home range size and movements of Laysan Teal. Variables included in the ANOVAs are described in further detail in the text. Significant P values ($P < 0.05$) are shown in bold.

Variables	**Fixed effects terms in ANOVA models**					
	Status[a]		**Year**[b]		**Status × Year**	
	$F_{1,23}$	P	$F_{1,23}$	P	$F_{1,23}$	P
Total home range (95% kernel)	**5.56**	**0.027**	1.91	0.180	0.94	0.342
Core home range (50% kernel)	3.88	0.061	3.31	0.082	2.44	0.132
Maximum distance between observations	3.56	0.072	**17.16**	**0.0004**	**6.61**	**0.017**
	Status[a]		**Time period**[c]		**Status × Time period**	
	$F_{1,13}$	P	$F_{2,11}$	P	$F_{2,11}$	P
Total home range (95% kernel)	4.45	0.055	1.09	0.370	0.46	0.644
Core home range (50% kernel)	3.49	0.085	3.67	0.060	1.22	0.332
Maximum distance between observations	1.08	0.328	**5.06**	**0.027**	0.09	0.910

[a] Status (*i.e.* breeding or nonbreeding) of individual Laysan Teal (n = 27, with two birds followed in both 2004 and 2005).

[b] Year (*i.e.* 2004, 2005) of data collection.

[c] Period (*i.e.* crepuscular, diurnal, nocturnal) of data collection.

Habitat use and behaviour

Laysan Teal showed highly significant differences in vegetation use and behaviour by time of day (Table 2, $P < 0.001$ for both variables). Of 910 vegetation-use records for 32 birds, the largest number (n = 211) of records was for birds located in *Eragrostis* habitat, followed by mixed *Eragrostis*-vine habitat (n = 165). Laysan Teal used the lake/mudflats and vine vegetation less frequently in the day than at other times (Table 3). Conversely, teal used shrub vegetation more during the day than during

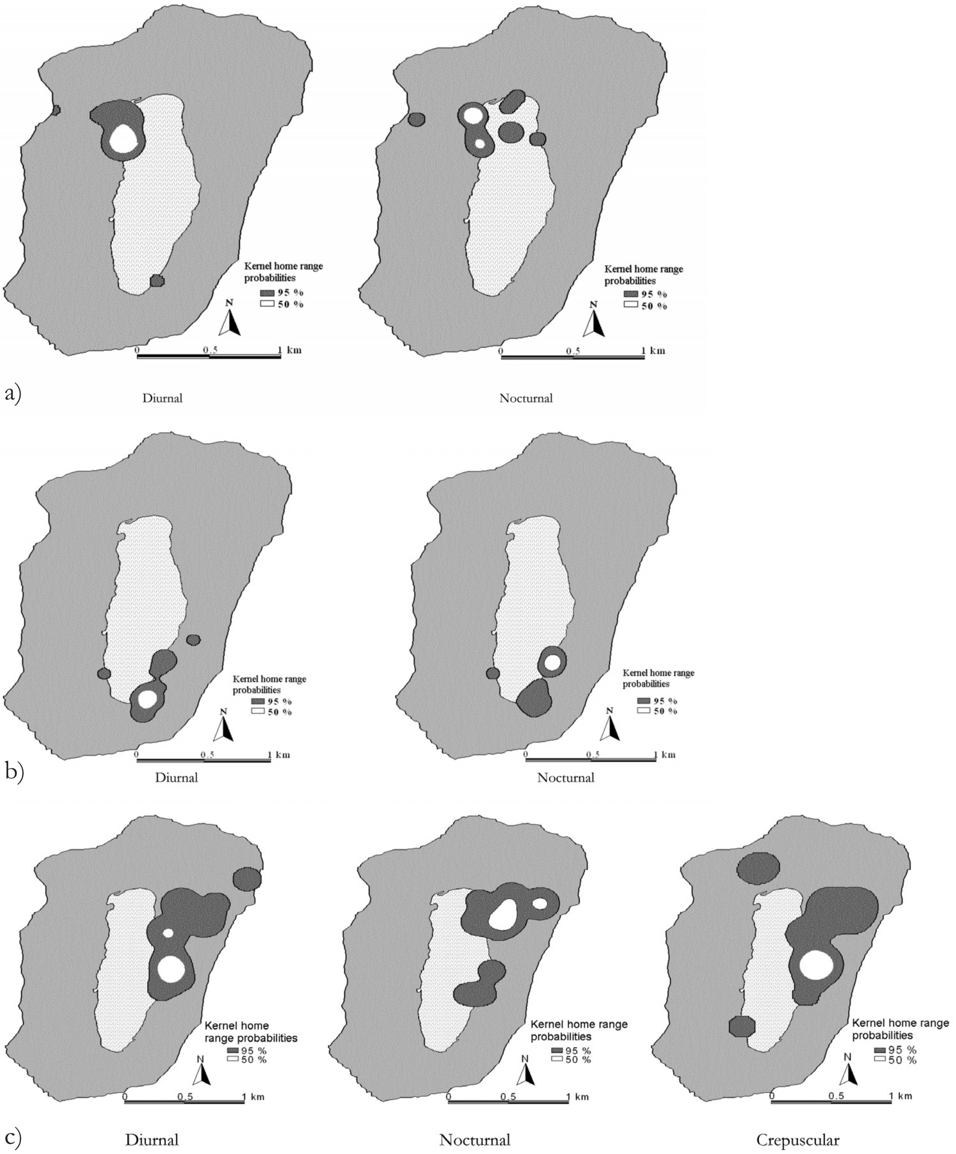

Figure 2. Home range (95% kernel) and core areas of use (50% kernel) of three representative female Laysan Teal *Anas laysanensis* on Laysan Island in 2005: a) diurnal (*n* = 25 locations) and nocturnal (*n* = 26 locations) home ranges of a nesting female (No. 334); b) diurnal (*n* = 27 locations) and nocturnal (*n* = 25 locations) home ranges of a non-nesting adult female (No. 563); and c) diurnal (*n* = 25 locations), nocturnal (*n* = 25 locations), and crepuscular (*n* = 28 locations) home ranges of a pre-breeder second year female (No. 545).

Table 2. Summary statistics (Wilk's Λ and P values) from multivariate analysis of variance (MANOVA) for compositional analysis of the effects of year, reproductive status, and time of day on habitat use by Laysan Teal. Variables included in the MANOVAs are described in further detail in the text. Significant P values ($P < 0.05$) are shown in bold.

Variables:	**Fixed effects terms in MANOVA models**													
	Status[a]		**Year**[b]		**Status × Year**		**Time period**[c]		**Status × Time period**		**Year × Time period**		**Status × Year × Time period**	
	Λ	*P*	Λ	*P*	Λ	*P*	Λ	*P*	Λ	*P*	Λ	*P*	Λ	*P*
Vegetation type	0.58	0.100	0.60	0.123	0.69	0.313	**0.35**	**<0.001**	0.73	0.390	0.64	0.100	0.65	0.118
Cover	0.91	0.488	**0.72**	**0.047**	0.88	0.374	0.80	0.082	0.83	0.161	0.89	0.439	0.78	0.0562
Behaviour	0.25	0.690	0.21	0.641	0.04	0.300	**0.28**	**<0.0001**	**0.65**	**0.0002**	**0.74**	**0.0067**	0.85	0.1809

[a] Status (*i.e.* breeding or nonbreeding) of individual Laysan Teal ($n = 27$).
[b] Year (*i.e.* 2004, 2005) of data collection.
[c] Period (*i.e.* crepuscular, diurnal, nocturnal) of data collection.

Table 3. Habitat use (mean log ratios) from multivariate analysis of variance (MANOVA) for compositional analysis of Laysan Teal use of vegetation types by time of day. Vegetation types used more than the *Eragrostis* reference point (0) have positive values for the mean log ratios, and those used less have negative values. Variables included in the MANOVAs are described in further detail in the text, along with methods and interpretation of the mean log ratios. Means that share a letter superscript within a vegetation type are not significantly different between time periods (Tukey multiple comparison procedure, $\alpha = 0.05$).

Variable:		**Diurnal**	**Nocturnal**	**Crepuscular**
Vegetation	*Eragrostis* (reference)	0.0	0.0	0.0
	Lake	-4.18^{a}	-1.88^{b}	-1.12^{b}
	Mixed w/ shrubs	-1.92^{a}	-2.76^{a}	-2.54^{a}
	Eragrostis-vine	-0.78^{a}	-0.57^{a}	-1.08^{a}
	Wetland	-4.07^{a}	-3.20^{a}	-4.02^{a}
	Mixed low	-3.29^{a}	-3.12^{a}	-2.95^{a}
	Shrubs	-0.94^{a}	-3.34^{b}	-2.44^{b}
	Vine	-2.43^{a}	-1.10^{ab}	-0.71^{b}
Cover	Full (>95%, reference)	0.0	0.0	0.0
	Heavy (71–94%)	-0.28^{ab}	0.34^{a}	-1.15^{b}
	Moderate (31–70%)	-0.15^{a}	0.11^{a}	-0.01^{a}
	Sparse (≤ 30%)	-0.59^{a}	-0.70^{a}	0.59^{a}

nocturnal and crepuscular periods (Table 3). *Eragrostis* was used more in the daytime, especially by incubating nesters. Most females (10 of 12; 73%) nested in *Eragrostis*. Two of 12 nests not placed in *Eragrostis* (one each in wetland sedges and vines) were crushed or exposed by Laysan Albatross *Phoebastria immutabilis*. Laysan Teal used all cover categories. Density of cover used did not differ significantly among time periods, but there was a tendency for birds to use full cover more during the day (Table 2) and heavy cover more at night than twilight hours (Table 2, n.s., means presented in Table 3). Teal used heavy cover significantly more in 2005 than 2004 (Table 4). Breeding status did not affect use of cover (Table 2).

Nearly half (49.7%) of the 937 behaviours were under cover ($n = 466$ observations of 30 birds), followed by search-forage (22.5%, $n = 211$). Incubation accounted for 9% of observations ($n = 87$) but these were not included in habitat analyses (MANOVA).

Table 4. Habitat use (mean log ratios) from multivariate analysis of variance (MANOVA) for compositional analysis of vegetation cover by year. Cover types used more than the *Eragrostis* reference point (0) have positive values for the mean log ratios, and those used less have negative values. Variables included in the MANOVAs are described in further detail in the text, along with methods and interpretation of the mean log ratios. Means that share a letter superscript within a cover category are not significantly different between time periods (Tukey multiple comparison procedure, $\alpha = 0.05$).

Cover	2004	2005
Full (> 95%, reference)	0.0	0.0
Heavy (71–94%)	-1.34^{a}	0.61^{b}
Moderate (31–70%)	-0.39^{a}	0.35^{a}
Sparse (≤ 30%)	-0.40^{a}	0.35^{a}

Laysan Teal behaviours also differed by time of day, with significant interactions between breeding status and time period (Table 2, $P < 0.001$). Non-breeders were more alert at night than nesters (Table 2, $P < 0.001$; Tukey's pair-wise $P < 0.01$). All Laysan Teal spent more time under cover diurnally than in other time periods (Fig. 3). Search-forage behaviour differed significantly by time period. Little time was spent foraging in the day, but foraging increased at twilight and the most foraging occurred at night (Fig. 3, Table 5). Additionally, birds search-foraged significantly more in 2004 (a dry year) than 2005 (a wet year; Table 5).

Rainfall and Brine Fly abundance

Mean daily rainfall from March–August 2005 (0.20 ± 0.04 cm/day, $n = 184$) was double that of the same months in 2004 (0.10 ± 0.03 cm/day, $n = 184$). Mean Brine Fly abundance differed between 2004 and 2005. An outlier of an unusual aquatic dipteran emergence (counts were an order of magnitude larger than any other date) was excluded and, after removing the outlier, 3.6 × more Brine Flies were observed in 2005 (270 ± 78 flies/sample, $n = 13$) than 2004 (75 ± 15 flies/sample, $n = 13$).

Discussion

Continental dabbling ducks' home ranges vary widely by species, individual bird, habitat, and season (reviewed in Baldassarre & Bolen 2006). It was expected that migratory anatid wintering and breeding home ranges would be larger than home ranges of most island ducks, but it is noteworthy that adult Laysan Teal's home ranges were generally > 100 times smaller than most dabbling duck home ranges (Clugston *et al.* 1994; Legagneux *et al.* 2009).

Laysan Teal's distribution of locations within home ranges, maximum distance

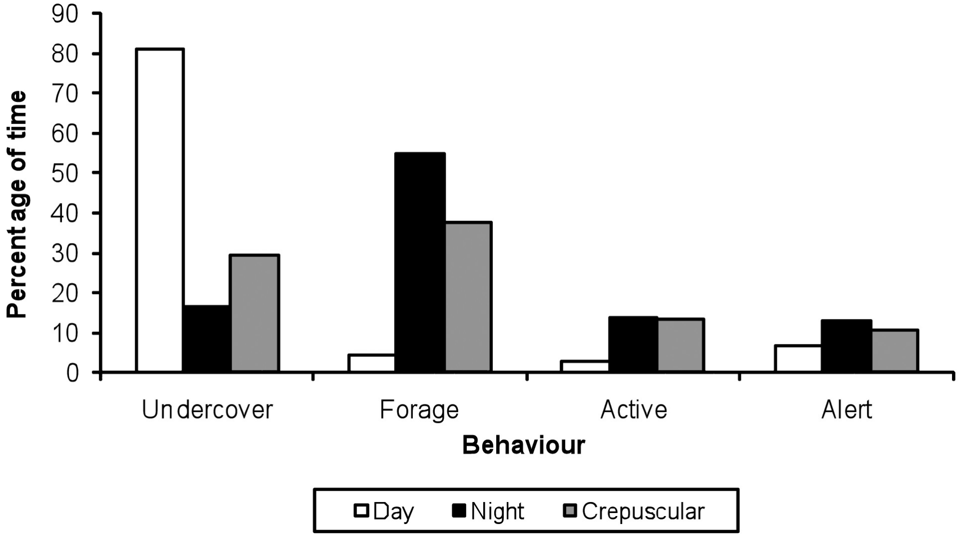

Figure 3. Time budget of instantaneous behaviours and frequency by time of day recorded while radio tracking Laysan Teal in 2004–2005 (*n* = 30 birds diurnal and crepuscular, *n* = 28 birds tracked nocturnally).

travelled, and behaviour were strongly affected by time of day. Habitat use can differ dramatically by time of day or in response to environmental variability (Munro *et al.* 2006). The limited overlap in diurnal and nocturnal core areas and circadian differences in habitat use and behaviour shown by these island ducks emphasize the importance of including the full range of activity in ecological studies. Given previous work on behavioural activity budgets (Marshall 1989; Reynolds 2002), it was expected that behaviours would vary within home ranges by time period. For most, core areas and habitats used for nocturnal foraging differed from those used for diurnal cover and nesting. The larger crepuscular movements compared with other times reflect the "commute" many birds make between diurnal undercover activities and nocturnal foraging sites. Circadian commuting behaviours are not typical of migratory waterfowl during the breeding season when most home range studies are made (Gilmer *et al.* 1975; Bruner 1997; Smith 2000). However, studies of continental dabbling ducks on wintering grounds report a daily commute between separate habitats: diurnal roost sites and nocturnal foraging sites. Long distance migrants also use distinctive habitats and have different ecological requirements in winter compared to the breeding season, with different spatial use attributable to divergent energy (reproduction *versus* survival) needs at these times (Legagneux *et al.* 2009).

Like some other waterfowl species (Gilmer *et al.* 1975; Bruner 1997; Baldassarre & Bolen 2006), home range size and movements were significantly affected by breeding status: non-breeders, including

Table 5. Behaviour (mean log ratios) from multivariate analysis of variance (MANOVA) for compositional analysis of effect of year × time of day on Laysan Teal activity. Behaviours used more than the "Under cover" reference point (0) have positive values for the mean log ratios, and behaviours used less have negative values. Variables included in the MANOVAs are described in further detail in the text, along with methods and interpretation of the mean log ratios. Means that share a lower case letter superscript within a behaviour group are significantly different between time periods (Tukey multiple comparison procedure, $\alpha = 0.05$). Means for a behaviour with an upper case letter superscript within a time period are significantly different between years (Tukey multiple comparison procedure, $\alpha = 0.05$).

Behaviour	Year	Diurnal	Nocturnal	Crepuscular
Under cover (reference)	2004	0.0	0.0	0.0
	2005	0.0	0.0	0.0
Alert	2004	-3.19^{a}	0.54^{Aabcd}	-2.43^{c}
	2005	-3.83^{b}	-3.77^{A}	-2.95^{d}
Active	2004	-3.97^{a}	–2.76	-0.48^{a}
	2005	–3.39	–1.33	–1.76
Loaf	2004	–2.96	–3.23	–3.58
	2005	–4.26	–4.56	–2.73
Search-forage	2004	-3.40^{a}	4.04^{abcA}	0.45^{abc}
	2005	-3.58^{b}	0.89^{abA}	-0.13^{abc}

second-year (SY) pre-breeders, generally had larger home ranges than nesters. The variability in the home range sizes, and distances travelled, were similar to those estimated from Laysan Teal tracked during breeding and non-breeding seasons 1998 to 2000 (mean total home range, 9.78 ± 2.6 ha, $n = 15$; Reynolds 2004). Both studies featured unpaired SY pre-breeders (a male in 1998, a female in 2005) with unusually large home ranges that were more than quadruple those of other Laysan Teal studied. Resightings data of marked birds and anecdotal observations also suggest that post-fledgling juveniles and pre-breeders make larger movements and more flights than most adult Laysan Teal. Thus, 'individual variation' described in home range sizes may be more predictable if the individuals' life history status (age, pair bond, and reproductive status) were known.

Laysan Teal used a diversity of habitats in different parts of their home range to satisfy different needs, from resting to foraging to breeding. On Laysan, dense vegetation cover, especially the sturdy lovegrass *Eragrostis* sp., was important for resting and incubating birds, whereas at night and crepuscular periods, birds used the lake and inland vines for foraging. Laysan Teal are sympatric with Laysan Albatross. Nesting females and downy ducklings are susceptible to trampling and harassment by large seabirds, and therefore need suitable cover and robust vegetation structure similar to *Eragrostis* when nesting in seabird colonies (Reynolds *et al.* 2007).

Differences in time spent foraging, prey taken, and habitats used for foraging, suggest a shift in optimal foraging strategy (Charnov 1976; Stephens & Krebs 1986) during dry compared with wet conditions on Laysan Island. Annual shifts in nocturnal foraging habitat were observed during an El Niño drought year (1998), when non-nesting birds spent more time in terrestrial habitats than in wetlands, whereas during the wet La Niña years (1999–2000) they spent more time in wetlands (Reynolds 2002). A similar interaction was predicted between habitat use and foraging behaviour between drier 2004 and wetter 2005, when Brine Flies were more abundant, but the differences were not quite significant. In this study, Laysan Teal spent more time foraging in 2004 than in 2005. They also foraged more at night in 2004 than they did in any other time period × year combination (*i.e.* they foraged more at night than during daytime or crepuscular periods in either year).

Management implications

As this study illustrates, the management of ecosystems to support endangered populations should consider all habitats used by animals during their circadian, seasonal and annual cycles for diverse activities including foraging, resting, nesting, brood rearing and moulting. The ecological needs of different demographic groups should also be taken into account. This is especially important for species with limited mobility, constraints on dispersal, or fragmented or anthropogenically restricted ranges, such as Laysan Teal.

Time spent foraging shifted as environmental conditions changed, indicating flexibility in Laysan Teal behaviour. This plasticity bodes well for conservation interventions, such as wild translocation, for this species, and perhaps for other non-migratory island endemics restricted to relictual ranges. Since many potential translocation sites do not have the same native-dominated vegetation communities as Laysan, and all other Hawaiian islands lack a hyper-saline ecosystem, managers will need to ensure that spatial and life history requirements are met in different habitats subject to environmental variability.

The use of multiple management actions is paramount to establishing a stable population that can withstand stochastic events such as disease outbreak and extreme weather. As Caughley (1994) recommends, the tools of managers should combine actions that increase numbers for small populations (translocations) while concurrently preventing population decline (habitat restoration).

Translocation sites should provide mammalian predator-free habitats (USFWS 2009), varied terrestrial and wetland habitats to incorporate nesting, resting, and moulting cover, and foraging habitat for adults and ducklings. Environmental variability influences food availability and the ability of birds to respond to changing conditions by adjusting their time budget or using alternate habitats (Reynolds 2002). Such opportunistic behaviour may help this non-migratory dabbling duck meet its foraging requirements within its restricted range.

Home range and population studies (Reynolds *et al.* 2008) from recently reintroduced birds on Midway Atoll, which has vegetation communities and a prey base distinct from Laysan's, indicate that the species uses novel habitats unavailable on Laysan. Nesting and foraging occurs in invasive weeds on Midway, and widespread removal of these "habitats" will require intensive vegetation restoration to meet the species' foraging, resting and nesting needs. Studies of Laysan Teal habitat use on Midway Atoll will provide interesting comparisons to expand our understanding of variation in the species' habitat requirements and space use and guide further conservation and habitat management.

Acknowledgements

We thank the U.S. Fish and Wildlife Service's refuge managers, including J. Leinecke, D. Palawski, B. Steglitiz, and C. Rehkemper, and also refuge biologist E. Flint and USFWS biotechnicians for assistance with field logistics and project implementation. S. Kropidlowski, J. Kelly, H. Major, and J. Shore helped attach transmitters on Laysan. We thank J. Breeden Jr. for radio-tracking in 2005 and for verifying the data. G. Pendleton, J. Walters, and two anonymous reviewers reviewed earlier versions of this manuscript and provided comments to improve it. P. Berkowitz assisted with ArcGIS analyses, and S. Nash helped format and edit this paper. This study was funded in part by the U.S. Geological Survey Wildlife Program, the U.S. Fish and Wildlife Service Ecological Services Pacific Islands Ecoregion, and the 2004/2005 USGS Quick Response Grants for population monitoring on Laysan. Staff and in-kind support were provided by the Hawaiian Islands National Wildlife Refuges. NOAA and its ship *Oscar Elton Sette* provided essential logistical support. L. Mehrhoff, past director of Pacific Island Ecosystems Research Center, facilitated funding and statistical support to complete this study. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.

Aldrich, J.W. 1980. *Selected Vertebrate Endangered Species of the Seacoast of the United States – Laysan Duck*. U.S. Fish and Wildlife Service Report No. FWS/OBS-80/01, USFWS, Washington, DC, USA.

Baldassarre, G.A. & Bolen, E.G. 2006. *Waterfowl Ecology and Management, 2nd edition.* Kreiger, Malabar, Florida, USA.

Beier, P., Vaughan, M.R., Conroy, M.J. & Quigley, H. 2006. Evaluating scientific inferences about the Florida panther. *Journal of Wildlife Management* 70: 236–245.

BirdLife International. 2009. *Anas laysanensis*. *In*: *IUCN 2010. IUCN Red List of Threatened Species*. Version 2010.2. http://www.iucnredlist.org. (accessed 7 July 2010).

Bruner, H.J. 1997. Habitat use and productivity of harlequin ducks in the Central Cascade range of Oregon. M.Sc. thesis, Oregon State University, Corvallis, Oregon, USA.

Bub, H. 1991. *Bird Trapping and Bird Banding*. Cornell University Press, Ithaca, New York, USA.

Burney, D.A., James, H.F., Burney, L.P., Olson, S.L., Kikuchi, W., Wagner, W.L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F., Gage, R.I. & Nishek, R. 2001. Holocene lake sediments in the Maha'ulepu caves of Kaua'i: evidence for a diverse biotic assemblage from the Hawaiian lowlands and its transformation since human arrival. *Ecological Monographs* 71: 615–642.

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

Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63: 215–244.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136.

Clugston, D.A., Longcore, J.R., McAuley, D.G. & Dupuis, P. 1994. Habitat use and movements of postfledging American black ducks (*Anas rubripes*) in the St. Lawrence estuary, Quebec. *Canadian Journal of Zoology* 72: 2100–2104.

Cooper, A., Rhymer, J., James, H.F., Olson, S.L., McIntosh, C.E., Sorenson, M.D. & Fleischer, R.C. 1996. Ancient DNA and island endemics. *Nature* 381: 484.

Ely, C.A. & Clapp, R.B. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. *Atoll Research Bulletin* 171: 361.

Gilmer, D.S., Ball, I.J., Cowardin, L.M., Riechmann, J.H., & Tester, J.R. 1975. Habitat use and home range of mallards breeding in Minnesota. *Journal of Wildlife Management* 39 (4): 781–789.

Gross, L. 2005. Why not the best? How science failed the Florida panther. *Plos Biology* 3: 1525–1531.

Guillemain, M., Fritz, H. & Duncan, P. 2002. The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. *Biological Conservation* 103: 183–198.

Herring, G., & Collazo, J.A. 2005. Habitat use, movements and home range of wintering Lesser Scaup in Florida. *Waterbirds* 28: 71–78.

Hooge, P.N. & Eichenlaub, B. 1997. *Animal Movement Extension to ArcView Version 1.1*. U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA.

Legagneux, P., Blaize, C., Latraube, F., Gautier, J. & Bretagnolle, V. 2009. Variation in home-range size and movements of wintering dabbling ducks. *Journal of Ornithology* 150(1): 183–193.

Lewis, T.L., Esler, D., Boyd, W.S. & Zydelis, R. 2005. Nocturnal foraging behavior of wintering Surf Scoters and White-winged Scoters. *Condor* 107: 637–647.

Marshall, A.P. 1989. *The Behavior of Laysan Ducks (*Anas laysanensis*) in Captivity and on Laysan Island.* Ph.D. Thesis, Ohio State University, Columbus, Ohio, USA.

Millspaugh, J.J., Gitzen, R.J., Kernohan, B.J., Larson, M.A. & Clay, C.L. 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32: 148–157.

Millspaugh, J.J., Skalski, J.R., Kernohan, B.J., Raedeke, K.J., Brundige, G.C. & Cooper, A.B. 1998. Some comments on spatial independence in studies of resource selection. *Wildlife Society Bulletin* 26: 232–236.

Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B. & Boyce, M.S. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87: 1112–1121.

National Oceanic and Atmospheric Administration & U.S. Fish and Wildlife Service. 2006. Northwestern Hawaiian Islands Marine National Monument. *Federal Register, 50 CFR Part 404* 71(167): 51134.

Olson, S.L. & Ziegler, A.C. 1995. Remains of land birds from Lisianski Island, with observations on the terrestrial avifauna of the Northwestern Hawaiian Islands. *Pacific Science* 49: 111–125.

Orians, G.H. & Soule, M.E. 2001. Introduction. *In* G.H. Orians & M.E. Soule (eds.), *Conservation Biology: Research Priorities for the Next Decade*, pp. 1–10. Island Press, Washington DC, USA.

Raim, A. 1978. A radio transmitter attachment for small passerine birds. *Bird Banding* 49: 326–332.

Rauzon, M.J. 2001. *Isles of Refuge.* University of Hawaii Press, Honolulu, Hawaii, USA.

Reynolds, M.H. 2002. *The Foraging Ecology, Population Dynamics, and Habitat Use of Laysan Teal (*Anas laysanensis*).* Ph.D. Thesis, Virginia Polytechnic and State University, Blacksburg, Virginia, USA.

Reynolds, M.H. 2004. Habitat use and home range of the Laysan Teal on Laysan Island, Hawaii. *International Journal of Waterbird Biology* 26: 183–192.

Reynolds, M.H., Crampton, L.H. & Vekasy, M.S. 2007. Laysan Teal nesting phenology and site characteristics on Laysan Island. *Wildfowl* 57: 54–67.

Reynolds, M.H., Seavy, N.E., Vekasy, M.S., Klavitter, J.L. & Laniawe, L.P. 2008. Translocation and post release demography of endangered Laysan Teal. *Animal Conservation* 11: 160–168.

Samuel, M.D. & Fuller, M.K. 1996. Wildlife radio telemetry. *In* T.A. Bookhout (ed.), *Research and Management Techniques, Fifth Edition*, pp. 370–417. The Wildlife Society, Bethesda, Maryland, USA.

SAS Institute. 2003. *SAS Software, Version 9.1.* SAS Institute, Cary, North Carolina, USA.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63: 739–747.

Seavy, N.E., Reynolds, M.H., Link, W.A. & Hatfield, J.S. 2009. Postcatastrophe population dynamics and density dependence of an endemic island duck. *Journal of Wildlife Management* 73: 414–418.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. *BioScience* 31: 131–134.

Smith, C.M. 2000. Population dynamics and breeding ecology of harlequin ducks in Banff National Park, Alberta, 1995–1999. Parks Canada Unpubl. Technical Report, Parks Canada, Banff, Alberta, Canada.

Southwood, T.R.E. 1978. *Ecological Methods, Second Edition.* Chapman and Hall, London, UK.

Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory.* Princeton University Press, Princeton, New Jersey, USA.

USFWS. 2009. *Revised Recovery Plan for the Laysan Duck (*Anas laysanensis*).* U.S. Fish and Wildlife Service Report, USFWS, Portland, Oregon, USA.

USGS. 2005. *Translocation of Endangered Laysan Ducks to Midway Atoll National Wildlife Refuge.* U.S. Geological Survey Report No. FS 2005-3128, USGS, Washington DC, USA.

Williams, M. 1996. Conservation dilemma with island waterfowl (Anatidae): a perspective based on the New Zealand experience. *Game and Wildlife* 13: 849–865.