Nesting ecology of the Hawaiian Duck *Anas wyvilliana* on northern Kaua‘i, Hawai‘i, USA

CHRISTOPHER P. MALACHOWSKI[1,*], BRUCE D. DUGGER[1], KIMBERLY J. UYEHARA[2] & MICHELLE H. REYNOLDS[3]

[1]Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97331, USA.

[2]U.S. Fish and Wildlife Service, Kaua‘i National Wildlife Refuge Complex, P.O. Box 1128, Kīlauea, Hawai‘i 96754, USA.

[3]Pacific Island Ecosystems Research Center, Kīlauea Field Station, Bldg. 344, P.O. Box 44, Hawai‘i National Park, Hawai‘i 96718, USA.

*Correspondence author. E-mail: christopher.malachowski@oregonstate.edu

Abstract

The nesting ecology of the endangered Hawaiian Duck *Anas wyvilliana* was studied on Kaua‘i, Hawai‘i, USA between 2012 and 2014. Radio-telemetry and other nest-searching techniques (*e.g.* foot searches, chain drags) were used to locate and characterise nest sites, and to estimate clutch size and nest success. Nests were found in upland areas associated with a variety of land cover types, including forests, Taro *Colocasia esculenta* agriculture, managed wetlands, grasslands and scrub/shrub (n = 29). Topographic features associated with nest sites included dikes, upland flats, dry wetland basins and mountain ridges. Distance between nests and water ranged from 0.1–100 m (mean ± s.e. = 26.7 ± 7.3 m; n = 22). Mean height of vegetation at the nests was 103 ± 15 cm, and median overhead cover class was for 66–95% concealment (n = 21). Ground cover within 1 m of nests in forest and scrub/shrub habitat was dominated by Wedelia *Sphagneticola trilobata*, Uluhe *Dicranopteris linearis*, Barbas de Indio *Andropogon bicornis* and California Grass *Urochloa mutica* (n = 9). Dominant plant species around nests in Taro agriculture primarily included Wedelia, Shortleaf Spikesedge *Kyllinga brevifolia* and Nodeweed *Synedrella nodiflora* (n = 8); ground cover in grassland was dominated by Wedelia, California Grass and Guinea Grass *Megathyrsus maximus* (n = 3). Birds initiated 96% of nests during the eight-month period from October–May inclusive, with 52% occurring during February through April (n = 23). No re-nests were confirmed; however, one radio-tagged female nested three times within a 14-month period, with nest attempts (two successful, one failed) six and eight months apart. Mean clutch size was 5.8 ± 0.4 eggs (range = 4–9; n = 19), and clutch size was higher during the wet season (November–April; 6.1 + 0.4 eggs) than the dry season (May–October; 4.5 ± 0.3 eggs). Nest success was 0.387 (95% CI =

0.150–0.623; n = 20). Causes of nest failure included complete depredation (n = 1), flooding (n = 1), and abandonment due to partial depredation or unknown reasons (n = 6).

Key words: clutch size, Hawai'i, Hawaiian Duck, island waterfowl, nest site characteristics, nest success.

The Hawaiian Duck *Anas wyvilliana* is a non-migratory, island-endemic species closely related to the widespread Mallard *A. platyrhynchos* and isolated Laysan Duck *A. laysanensis* (Lavretsky *et al.* 2015). Once relatively common throughout the main Hawaiian Islands, it has undergone considerable range contractions and population declines during the past century due to habitat loss, introduced predators, overhunting and genetic introgression with feral Mallard (Engilis Jr. *et al.* 2002; United States Fish and Wildlife Service [USFWS] 2011). The present range of non-hybridised Hawaiian Duck is restricted primarily to the islands of Kaua'i and Ni'ihau (USFWS 2011). Although listed as endangered by the U.S. Fish and Wildlife Service and the International Union for Conservation of Nature, most fundamental aspects of Hawaiian Duck ecology and population demography remain poorly understood (Swedberg 1967; Engilis Jr. *et al.* 2002; BirdLife International 2016). In particular, little is known about the nesting ecology of the species, and this lack of information limits efforts to implement sound management and conservation measures for Hawaiian Duck recovery plans (USFWS 2011).

Information on the nest site characteristics and reproductive vital rates for Hawaiian Duck is scant. Qualitative records based largely on brood observations reveal that Hawaiian Duck breed at a range of elevations (sea level to 1,658 m; Swedberg 1967; Giffin 1983), and limited direct nest observations suggest that Hawaiian Duck nest in association with a variety of land cover types, topographic features and vegetation types (Schwartz & Schwartz 1953; Swedberg 1967; Giffin 1983; Engilis Jr. *et al.* 2002; Gee 2007). However, the only study that has quantified vegetation characteristics and visual obscurity at Hawaiian Duck nest sites reported on a small sample of nests (n = 7) which were mostly found incidentally during other activities (Gee 2007) and, therefore, reflect a biased subset of potential nest locations. Estimates of clutch size for wild Hawaiian Ducks are similarly based on a small sample of nests (n = 17; Munro 1944; Richardson & Bowles 1964; Swedberg 1967; Gee 2007), or are from a population that was comprised of hybrids (Chang 1990), and no estimates for nest success rates are available (Engilis Jr. *et al.* 2002). Nest success (*i.e.* the percentage of nests in which at least one egg hatched), can be one of the most important factors affecting population growth of upland nesting duck species (Johnson *et al.* 1992; Hoekman *et al.* 2002; Howerter *et al.* 2014), and estimates of key vital rates, such as clutch size and nest success, are necessary to develop accurate population models for assessing population trends, population viability, and vulnerability to specific threats, as well as aiding the management decision process (Williams *et al.* 2002).

In this study, we used both radio-telemetry and other nest-searching techniques (*e.g.* foot searches, chain drags) to locate nests and investigate the breeding ecology of Hawaiian Duck on Kaua'i. Our primary objectives were to: (1) describe the characteristics of their nest sites, and (2) record clutch sizes and nest success rates. This information will fill an important void in our understanding of the species and may aid managers tasked with managing and restoring habitat for the endangered Hawaiian Duck.

Methods

Study area

Research was conducted at Hanalei National Wildlife Refuge (NWR) and adjacent areas in the north-central region of Kaua'i, Hawai'i (22.205°N, 159.475°W). Major rivers on the north shore of Kaua'i, such as the Hanalei River, form in the central mountains of the island (maximum elevation 1,598 m) and flow northward as they cut through deep, steep-sided valleys that open into broad floodplains in the coastal lowlands before emptying into the Pacific Ocean (MacDonald *et al.* 1960). Established in 1972, Hanalei NWR is situated in the floodplain of the lower Hanalei River and is characterised by managed and unmanaged palustrine emergent wetlands, flooded agricultural fields used for the production of Taro *Colocasia esculenta*, ephemerally flooded pastures and grassland, riverine habitat, and forested hillsides. Refuge wetlands are managed year-round to provide habitat for Hawaiian Duck and three other endangered Hawaiian waterbirds, including Hawaiian Coot *Fulica alai*, Hawaiian Common Gallinule *Gallinula galeata sandvicensis* and Hawaiian Black-necked Stilt *Himantopus mexicanus knudseni* (USFWS 2011). Taro farming occurs at Hanalei NWR under a special-use permit. Taro is a traditional Hawaiian food crop and farmed in shallowly flooded fields, or lo'i, similar to rice paddy fields. Dominant plant species in seasonal wetlands included Fimbry *Fimbristylis littoralis*, Mexican Primrose-willow *Ludwigia octovalvis*, California Grass *Urochloa mutica*, Barnyard Grass *Echinochloa crus-galli* and Vasey's Grass *Paspalum urvillei* (Malachowski & Dugger 2018), and river banks were generally dominated by Hau *Talipariti tiliaceum* and California Grass. Forested hillsides and ridges predominantly contained Common Guava *Psidium guajava*, Strawberry Guava *Psidium cattleianum*, Albizia *Falcataria moluccana*, Kukui *Aleurites moluccanus*, Mango *Mangifera indica*, Tahitian Screwpine *Pandanus tectorius*, Silky Oak *Grevillea robusta*, Java Plum *Syzygium cumini* and Uluhe *Dicranopteris linearis*.

Rainfall on Kaua'i is primarily orographic, varying substantially with elevation and between windward (northeast) and leeward (southwest) sides of the island (MacDonald *et al.* 1960). Mean annual rainfall (1938–2011) at Princeville Ranch, approximately 1 km north of Hanalei, NWR is 204 cm/year, allocated between a wet season (November–April, 20 cm/month) and a slightly drier season (May–October, 15 cm/month; National Climate Data Center

[NCDC], www.ncdc.noaa.gov, accessed 01 Aug 2017). Temperatures in this region (1999–2011) fluctuated little throughout the year, and mean monthly low and high temperatures were 19.1° and 27.6°C, respectively (NCDC).

Capturing and marking Hawaiian Ducks

During 22 November–14 December 2012 and 29 November–19 December 2013, birds were captured using customised baited swim-in traps (Hunt & Dahlka 1953; Dugger & Malachowski 2013) and ringed with a U.S. Geological Survey (USGS) metal leg band (Gustafson *et al.* 1997). Sex and age were determined by using cloacal examination and plumage characteristics (A. Engilis Jr., University of California-Davis, unpubl. data). Mass and culmen length were measured for each bird, and body condition indices (Body Condition Index [BCI] = body mass/bill length; Harder & Kirkpatrick 1996) were used as an indirect measure of physiological condition.

Radio transmitters (AI-2M, Holohil Systems) were implanted intracoelomically in 50 adult female Hawaiian Ducks (n_{2012} = 34, n_{2013} = 16) using procedures described by Korschgen *et al.* (1984, 1996). Transmitters were not attached to birds undergoing remigial moult, birds that were gravid or had brood patches, or any bird whose BCI was in the lower 10th percentile for the species based on data collected during previous trapping efforts (n_{female} = 96; C.P. Malachowski, Oregon State University, unpubl. data). Transmitters weighed 18 g and were configured to have a percutaneous antenna, 18 month battery life, and a mortality sensor that activated after 12 h of inactivity. Following surgery, birds were allowed to recover for at least 60 min prior to being released at their capture site. All capture and sampling procedures were approved under USFWS Threatened and Endangered Species permit TE-702631 (sub-permits KNWR-7, KNWR-8, and KNWR-9), USFWS Region 1 Migratory Bird Depredation permit MB120267-1, Federal Bird Banding permit 23718, State of Hawai'i Protected Wildlife permit WL15-02, and Oregon State University Institutional Animal Care and Use Committee permits 4072 and 4494. Access to Hanalei NWR was granted by the USFWS.

Locating and monitoring nests

Between December 2012 and December 2014, radio-tagged female Hawaiian Ducks were tracked to locate and monitor nests using a truck-mounted, null-peak antenna system (four-element) or handheld three-element antenna. Attempts were made to locate individuals at least once per day, 5–7 days per week until mortality occurred, the transmitter failed, the transmitter was extruded, or our field season terminated in December 2014. If a female was suspected of initiating a nest, suggested by the bird remaining in the same location for approximately three consecutive days or repeatedly during a day, the location was marked with a GPS unit, and the putative nest area was searched when the female was absent. To supplement the sample of nests found via radio-telemetry, additional nests for non-tagged birds were located at Hanalei NWR using periodic and systematic foot searches (*i.e.* walking transects while striking the vegetation with bamboo switches), rope drags, and chain drags (Klett *et al.* 1986), as well as using observations of females in or near possible nesting cover and incidentally while performing other tasks.

During the first visit to each nest, the number of eggs was recorded and the incubation stage was estimated by egg candling (Weller 1956). If nests were found during the egg-laying period, they were revisited during early incubation to record final clutch size. Nests of radio-tagged females were monitored every 1–2 days via telemetry and periodically revisited when females were absent to monitor nest contents. Nests were revisited for a final time after the clutch hatched or the nest failed, indicated by telemetry (*e.g.* female absence from the nest for 2–3 days). Nests of non-tagged females were monitored approximately every 3–7 days when birds were off nests if low visual obscurity allowed observers to detect bird presence/absence without flushing the bird; otherwise, nests were revisited after the projected hatch date (see Data analyses). Length and breadth of eggs were measured to the nearest 0.1 mm with dial callipers during incubation or after nest failure or hatching. Nests were designated as successful (≥ 1 egg hatched) or failed (Cowardin *et al.* 1985). Apparent causes of nest failure were classified as abandonment, depredation, flooding or human-caused destruction.

Characterising nest sites

During the first and last visit to nests, distance to nearest water was measured, and canopy cover above the nest was estimated by looking down on the nest bowl from 1 m above and classified as 0 (< 5% cover), 1 (5–35%), 2 (36–65%), 3 (66–95%), or 4 (> 95%). Land cover type at each nest location was classified as grassland, scrub/shrub, pasture, forest, managed wetland, Taro agriculture or developed open area. For general descriptive purposes, the topographic feature associated with nests was recorded as upland flat, dike, island, wetland basin or ridges. Wetland basins were dry, fallow Taro lo‘i or managed wetland impoundments.

To prevent disturbance or abandonment of nesting birds, the following nest site characteristics were measured or described only after clutches hatched or nests failed: nest dimensions (including depth and diameter of nest bowl and cup) and composition, height of vegetation above the nest, concealment values, visual obstruction readings, and ground cover and species composition within 1 m and 15 m radii. Nest concealment values (0–4) were assigned according to the percentage of nest that was concealed from a height and distance of 1 m in each of the four cardinal directions, using the scoring system previously described for canopy cover. These four concealment values were then averaged for each nest. Visual obstruction readings (VORs) were estimated using a vegetation profile board (2.0 m high × 0.3 m wide) that was divided vertically into four 0.5 m sections and centred over the nest (Nudds 1973). Scores were assigned by estimating the percentage of each 0.5 m section that was obstructed from a height of 1 m and distance of 15 m in each of the four cardinal directions (1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–

100%). Scores from all directions were averaged for each 0.5 m interval, resulting in four height-specific VORs for each nest. Percent of ground cover by individual plant species, bare ground and water were estimated within 1 m and 15 m radii of nests. Species nomenclature followed the Integrated Taxonomic Information System on-line database (www.itis.gov, accessed 22 May 2018). Ground cover was classified into eight vegetation categories: fern, forb, grass, sedge, shrub or tree, vine, bare ground and open water. Ground cover composition (by species and vegetation categories) was summarised by land cover type. Nests that were inactive when first located or influenced by anthropogenic activities (*e.g.* mowed over) were eliminated from the sample of nests used to estimate all nest site characteristics, except land cover type and topographic feature.

Data analyses

Nest initiation date (*i.e.* start of egg-laying) was calculated for each nest that was active when found using a combination of clutch size, incubation stage and hatch date (when applicable) assuming females laid one egg per day (Alisauskas & Ankney 1992), began incubating when the last egg was laid, and incubated nests for 28 days (Swedberg 1967). If the nest initiation date could only be narrowed down to a range of dates, the midpoint of that range was used. Only incubated clutches were used in clutch size analyses. For both clutch size and nest initiation date calculations, it was assumed that no partial nest depredation occurred prior to locating the nest, unless evidence indicated otherwise (*e.g.* presence of broken eggshells). Two-tailed *t*-tests were used to compare clutch size between years (2013 *vs.* 2014) and tagging status (radio-tagged *vs.* non-tagged). A one-tailed *t*-test was used to test the hypothesis that clutch size was greater during months associated with the wet season (November–April) compared to the dry season (May–October) based on long-term climate data (1938–2011; NCDC), because rainfall is often linked to resource availability, breeding activity, and reproductive performance for tropical and subtropical ducks (Immelmann 1971; Reynolds *et al.* 2007; Bielefeld *et al.* 2010). Because long-term climate patterns often differ from the contemporaneous conditions which a bird experiences, we used Pearson correlation analysis to evaluate the effects of total rainfall within 30 days prior to nest initiation on clutch size. Climate data was obtained from a USGS climate station at Princeville Ranch, approximately 1 km north of Hanalei NWR (NCDC). P values < 0.05 were designated significant. Clutch sizes were reported as $\bar{x} \pm$ s.e.

Daily nest survival rate ($\hat{S}_i$) was estimated using the likelihood-based nest survival model in Program MARK (White & Burnham 1999; Dinsmore *et al.* 2002). Five single-variable candidate models and an intercept-only (null) model were developed to explain possible variation in daily nest survival rates of Hawaiian Duck. Variables included year (2013, 2014), season (wet, dry), transmitter status (tagged, non-tagged), nest concealment from 1 m and overhead nest concealment. Season was assigned to each nest based on the timing of nest initiation (wet: Nov–April; dry: May–Oct). Nest concealment categories included well-concealed (≥ 3, based on previously described scoring system) and moderately to poorly concealed (< 3). Akaike's information criterion values adjusted for small sample sizes (AIC_c; Hurvich & Tsai 1995) and AIC_c weight were used to select the most parsimonious models (Burnham & Anderson 2002). Models with ≤ 2.0 ΔAIC_c of the top-ranked model were considered competitive, and 95% confidence intervals for covariate effect sizes were used to interpret results. Nest success was calculated by extrapolating daily nest survival to 34 days (6 days for egg laying + 28 days of incubation) under the assumption that nest survival was constant across both stages. Nests that were destroyed by investigators (n = 1) were excluded from nest survival analysis.

Results

Between 2012 and 2014, 50 adult female Hawaiian Ducks were radio-tagged. Mean body mass (± s.e.) of tagged birds was 660 ± 8 g (range = 575–780), and transmitter mass averaged 2.7 ± 0.03% (range = 2.3–3.1%) of female body mass. All birds survived transmitter implantation surgery, and birds were tracked for an average of 283 ± 23 days (median = 243 days; range = 10–708).

Twenty-nine nests, including six initiated by radio-tagged females and 23 initiated by non-tagged females, were located during the two-year study. Nesting for at least three additional radio-tagged birds was inferred from radio-telemetry data, but these nests were not located and, therefore, were omitted in the summary statistics. Additional radio-tagged females may have nested on private property where landowners prohibited access. Nests of non-tagged females were found using foot searches (n = 7), rope or chain drags (n = 2), and incidentally while performing other tasks (n = 14). Of the 29 nests located, 20 were first visited during incubation and three during laying. Six nests were first located after hatching or failure and were used only for describing broad-scale nest site characteristics (*i.e.* land cover type, topographic feature).

Nest sites characteristics

Nests were found in upland areas associated with a variety of land cover types, including Taro (n = 13), forest (n = 8), managed wetlands (n = 4), grassland (n = 3), and scrub/shrub (n = 1). Topographic features associated with nest locations included dikes (n = 13, including 11 in Taro and 2 in managed wetlands), upland flats and gently sloping hills (n = 9, including 5 in forest, 3 in grassland, and 1 in scrub/shrub), dry wetland basins (n = 4, including 2 in Taro and 2 in managed wetlands), and mountain ridges (n = 3). The three nests found on forested ridges were approximately 30 m above sea level. Nests initiated by radio-tagged females (n = 6) were placed in forested cover (83%) and Taro (17%). Mean distance to nearest water was 26.7 ± 7.3 m and ranged from 0.1 to 100 m (n = 22).

Hawaiian Ducks generally nested on the ground, but one nest was built on an elevated platform under Barbas de Indio *Andropogon bicornis*, suspended by Wedelia *Sphagneticola trilobata* and Barbas de Indio. Nests were constructed of the stems, leaves and seed pod casings of nearby species of vegetation and lined with variable amounts of down. Nest cup and nest bowl metrics were recorded for 20 nests that were active when first found. Mean nest bowl diameter was 27 ± 1 cm (range: 21–38), and mean depth was 9 ± 0.5 cm (range: 5–14). Mean nest cup diameter was 15 ± 0.5 cm (range: 12–20), and mean depth was 6 ± 0.3 cm (range: 4–10).

Mean height of ground vegetation above nests was 103.0 ± 15.1 cm (range = 31–344; *n* = 21), and the mean nest concealment score from 1 m was 3.1 ± 0.2 (*i.e.* ~66–95% concealed; *n* = 21). Nests were also generally well concealed from above, although overhead cover varied: 19% of nests had overhead canopy coverage of > 95%, 43% were 66–95% concealed, 10% were 36–65% covered, 19% were 5–35% covered, and 10% were clearly visible (< 5% cover). The mean overhead cover score was 2.4 ± 0.3 (median = 3; *n* = 21) during final nest visits, remaining similar to overhead cover recorded at the time of the first nest visit (mean = 2.4 ± 0.3; median = 3; *n* = 19). VORs were 4.7 ± 0.2, 3.5 ± 0.3, 2.7 ± 0.4 and 2.4 ± 0.4 in the 0.5 m, 1.0 m, 1.5 m and 2.0 m intervals, respectively (*n* = 20).

Ground cover within 1 m of nests (*n* = 21) primarily consisted of forbs and grasses (68% combined; Table 1). The most abundant plant species within 1 m of nests, comprising a total mean ground cover of 77%, included Wedelia, Uluhe, California Grass, Shortleaf Spikesedge *Kyllinga brevifolia* and Barbas de Indio; all other species comprised less than 5.0% each in mean ground cover (Table 2). However, ground cover composition varied among habitat types. Nests located in forests and scrub/shrub habitat were dominated by forbs, ferns and grasses (95% combined), while nests in Taro were dominated by forbs and sedges (80%), and nests in grassland were placed amongst forbs and grasses (98%; Table 1). Dominant plant species within 1 m of nests in forest and scrub/shrub habitat included Wedelia, Uluhe, Barbas de Indio and California Grass (93% combined; Table 2). On Taro dikes and in fallow lo‘i, ground cover around nests primarily included Wedelia, Shortleaf Spikesedge, Nodeweed *Synedrella nodiflora*, Fimbry and California Grass (77% combined), and ground cover in grassland was dominated by Wedelia, California Grass and Guinea Grass *Megathyrsus maximus* (96% combined; Table 2).

Ground cover within 15 m of nests (*n* = 20) primarily included forbs, grasses and ferns (76% combined), followed by five other ground cover types (Table 1). Nests in Taro were situated amongst forbs, grasses and open water (86% combined), while nests in forest and scrub/shrub habitat were amongst forbs, ferns, grasses, and shrubs and trees (96% combined), and nests in grasslands were amongst forbs and grasses (84% combined). Nests were located under varying amounts of tree canopy cover.

Nest initiation, clutch size, and egg size

Nest initiation dates were determined for 23 nests and clutch size for 19 nests. Combining data among years, birds initiated 96% of nests during the eight-month period from October through May, with 52% occurring during February through April. More nests were found during the wet season (*i.e.* November–April; 74%)

Table 1. Ground cover composition (%) within 1 m and 15 m of Hawaiian Duck nests in four land cover types on Kaua'i, Hawai'i USA, 2013–2014.

		Forest and scrub/shrub		Grassland		Managed wetland		Taro		Overall	
Plot radius	**Category**	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.
1 m	Ferns	34.3	16.3	0.3	0.3	0.0		0.0	0.0	14.8	7.8
	Forbs	36.0	12.0	62.7	19.2	42.0		52.8	12.9	46.5	7.6
	Grasses	24.8	11.5	35.3	17.2	51.0		8.9	5.0	21.5	6.1
	Sedges	0.0	0.0	0.0	0.0	7.0		27.4	14.2	10.8	6.0
	Shrubs and trees	3.2	1.8	0.0	0.0	0.0		6.2	4.4	3.7	1.8
	Vines	1.7	1.7	1.7	1.7	0.0		0.0	0.0	1.0	0.7
	Bare ground	0.0	0.0	0.0	0.0	0.0		0.6	0.6	0.2	0.2
	Open water	0.0	0.0	0.0	0.0	0.0		4.0	3.7	1.5	1.4
	n	9		3		1		8		21	
15 m	Ferns	27.3	11.8	7.3	4.3	0.0		0.0	0.0	13.4	5.9
	Forbs	29.1	9.4	48.3	12.8	21.6		46.7	5.9	37.8	5.3
	Grasses	19.8	7.4	35.3	7.3	40.0		25.3	4.5	25.1	3.9
	Sedges	0.9	0.9	0.3	0.3	38.0		8.3	2.7	5.3	2.1
	Shrubs and trees	19.3	4.1	2.0	1.1	0.0		2.2	1.1	9.8	2.7
	Vines	0.1	0.1	1.3	1.3	0.0		0.1	0.1	0.3	0.2
	Bare ground	2.1	1.1	2.3	1.5	0.4		3.4	2.2	2.5	0.9
	Open water	1.4	0.8	3.3	3.3	0.0		13.9	4.2	6.0	2.0
	n	9		3		1		7		20	

Table 2. Ground cover composition by species (%) within 1 m of Hawaiian Duck nests (n = 21) in four land cover types on Kaua'i, Hawai'i, USA, 2013–2014. Only species that comprise ≥ 2% mean cover for at least one land cover type are included.

	Forest and scrub/shrub (n = 9)		**Grassland** (n = 3)		**Managed wetland** (n = 1)		**Taro** (n = 8)		**Overall** (n = 21)	
Species	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.
Wedelia *Sphagneticola trilobata*	35.6	11.8	61.0	20.8	20.0		35.0	13.7	38.2	7.7
Uluhe *Dicranopteris linearis*	32.9	16.4	0.0	0.0	0.0		0.0	0.0	14.1	7.7
California Grass *Urochloa mutica*	11.0	10.9	22.0	5.1	10.0		5.4	5.0	10.4	5.0
Shortleaf Spikesedge *Kyllinga brevifolia*	0.0	0.0	0.0	0.0	0.0		21.8	11.2	8.3	4.7
Barbas de Indio *Andropogon bicornis*	13.8	7.1	0.0	0.0	0.0		0.0	0.0	5.9	3.3
Nodeweed *Synedrella nodiflora*	0.0	0.0	0.0	0.0	0.0		9.4	9.4	3.6	3.6
Fimbry *Fimbristylis littoralis*	0.0	0.0	0.0	0.0	5.0		5.6	5.6	2.4	2.1
Guinea Grass *Megathyrsus maximus*	0.0	0.0	13.3	13.3	0.0		0.4	0.4	2.0	1.9
Climbing Dayflower *Commelina diffusa*	0.0	0.0	1.7	1.7	5.0		4.0	2.0	2.0	0.9
Hilo Grass *Paspalum conjugatum*	0.0	0.0	0.0	0.0	21.0		2.2	2.2	1.9	1.3
Open water	0.0	0.0	0.0	0.0	0.0		4.0	3.7	1.5	1.4
Shoebutton *Ardisia elliptica*	0.0	0.0	0.0	0.0	0.0		3.0	2.0	1.1	0.8
Mexican Primrose-willow *Ludwigia octovalvis*	0.0	0.0	0.0	0.0	15.0		0.9	0.7	1.1	0.8
Barnyard Grass *Echinochloa crus-galli*	0.0	0.0	0.0	0.0	20.0		0.0	0.0	1.0	1.0
Manyspike Flatsedge *Cyperus polystachyos*	0.0	0.0	0.0	0.0	2.0		0.0	0.0	0.1	0.1

compared to the dry season (26%). No re-nests were confirmed. One radio-tagged female nested three times within a 14-month period, however, with nests initiated in February 2013 (5 of 7 eggs hatched), October 2013 (3 of 4 eggs hatched) and April 2014 (4 egg clutch failed). All nest sites for this bird were within 24 m of each other.

Mean clutch size was 5.8 ± 0.4 eggs (range = 4–9; mode = 4; $n = 19$). Clutch size was higher during the wet season (6.1 ± 0.4; $n = 15$) than the dry season (4.5 ± 0.3; $n = 4$; $t_{17} = 1.97$, $P < 0.05$), but was not positively associated with total rainfall within 30 days prior to initiating nests ($r = -0.18$, n.s.). Clutch sizes did not differ between years or between radio-tagged and non-tagged females ($t_{17} = 0.97$ and -1.33, respectively; n.s. in each case). Mean egg length was 54.8 ± 0.6 (range = 50.8–64.7; $n = 33$), and mean egg width was 37.8 ± 0.2 (range = 35.6–39.5; $n = 33$).

Nest survival

The sample of nests available for survival estimation was 20. Of six candidate models, the top-ranked model was the null model (*i.e.* constant survival). Models including effects of season, year, transmitter attachment, and nest concealment fell within 2 ΔAIC_c of the top model; however, the 95% confidence intervals for the β coefficients broadly overlapped zero, and these parameters were therefore not significant. Daily nest survival rate based on the intercept-only model was 0.972 (95% CI = 0.946–0.986), and overall nest survival for the 34 day nesting cycle was 0.387 (95% CI = 0.150–0.623). Causes of nest failure included complete depredation ($n = 1$), flooding ($n = 1$) and abandonment due to partial depredation or unknown reasons ($n = 6$). Partial nest depredation did not always lead to abandonment, and at least two females continued incubating nests through hatching after 1–2 eggs were depredated.

Discussion

Our study reveals that Hawaiian Ducks nest in association with a variety of land cover types and topographic features. Although the sample of nests initiated by non-transmittered birds may represent a biased subset of potential nest locations, the sample of nests of tagged birds can be considered largely unbiased, and these data suggest that forested cover, including ridges and upland flats, is likely important for nesting birds. Five of six confirmed nests (and two of three inferred nests) of radio-tagged birds were placed in forested areas. Given the abundant and variable precipitation on Kaua‘i throughout the year, the use of forested slopes by nesting birds may be a response to flooding in low elevation depressions and flats. For example, one nest placed in a fallow Taro lo‘i was washed out during a flood event in 2013. If certain characteristics of fallow lo‘i or wetland impoundments lead to nest site selection, these flood-prone locations may function as ecological traps (Dwernychuk & Boag 1972; Schlaepfer *et al.* 2002).

Similar to closely-related Mallard, Laysan Duck and Mottled Duck *Anas fulvigula*, Hawaiian Duck generally nested in dense vegetation with moderate to high concealment from above and laterally (Moulton & Weller 1984; Drilling *et al.* 2002;

Reynolds *et al.* 2007; Bielefeld *et al.* 2010). Also consistent with these other species, dominant vegetation types at nest sites included forbs and grasses (Moulton & Weller 1984; Drilling *et al.* 2002; Reynolds *et al.* 2007; Bielefeld *et al.* 2010); however, ferns, such as the native Uluhe, comprised a substantial proportion of ground cover at some forested nest sites. Uluhe forms dense thickets exceeding 3 m in height (Russell *et al.* 1998) and may provide protection from mammalian predators by concealing nests and limiting ease of access (VanZandt *et al.* 2014). Across all land cover types, Wedelia was the most abundant and commonly encountered species within 1 m of nests, accounting for 38% cover on average and occurring at 62% of nests. Wedelia, a non-native and naturalised species on Kaua'i, forms dense and tangled mats up to 30 cm in height (Thaman 1999; Qi *et al.* 2014). Although providing nest concealment and structure, Wedelia may present potential risks (*e.g.* entanglement, barriers) for ducklings leaving nests, particularly in areas where extensive monocultures form.

Our estimate of mean clutch size (5.8 eggs) was lower than the minimum clutch size reported for females on Kaua'i and O'ahu during the 1940s and 1960s (range = 6–10 eggs, mean = 8.3, n = 11 nests; Munro 1944; Richardson & Bowles 1964; Swedberg 1967). Lower clutch sizes could reflect poor or crowded foraging conditions or poor individual body condition (Krapu & Swanson 1975; Eldridge & Krapu 1988; Alisauskas & Ankney 1992; Johnson *et al.* 2002; Krapu *et al.* 2004). However, reduced clutch sizes may also be a function of increased nesting attempts throughout the year (Duncan 1987; Eldridge & Krapu 1988; Krapu *et al.* 2004). Changes to wetland habitat management on Kaua'i (*e.g.* Hanalei NWR), particularly over the past two decades, has resulted in additional year-round wetland resources for waterbirds (USFWS 2011; Malachowski & Dugger 2018), potentially providing opportunities for additional nesting attempts. Although we did not document any renesting attempts, one radio-tagged female nested three times within a 14-month period, a pattern consistent with a sub-annual breeding strategy (Chapin 1954; Ashmole 1968; Reynolds *et al.* 2014). Two of these three nesting attempts were successful; however, we were unable to monitor fledging success. Additional work is needed to determine if this nesting pattern represents an anomaly or the norm for Hawaiian Duck. Mean egg dimensions of Hawaiian Duck (54.8 × 37.8 mm) were similar to measurements previously reported (56.5 × 38.6 mm; Engilis Jr. *et al.* 2002; Gee 2007).

Nest success of Hawaiian Duck (39%) was high compared to Mallard (generally < 10–15%) and Mottled Duck (6–28%) breeding in continental North America (Walters 2000; Durham & Afton 2003; Dugger *et al.* 2010; Varner *et al.* 2013; Walker *et al.* 2013; Howerter *et al.* 2014). Nest survival of 15% has been reported to maintain stable populations of Mallard (Cowardin *et al.* 1985; Greenwood *et al.* 1995), and the comparatively high nest survival of Hawaiian Duck suggests that this demographic rate may not be currently constraining recruitment. However, Hawaiian Duck laid smaller clutches compared to Mallard and Mottled Duck

(5.8 *vs.* 8.7 and 9.2 eggs, respectively; Drilling *et al.* 2002; Johnson *et al.* 2002). Estimates for additional demographic parameters, such as nesting propensity and duckling and adult survival, are necessary to better understand the implications of our nest success and clutch size estimates for Hawaiian Duck population dynamics.

Unlike continental dabbling ducks, nest abandonment was the most common cause of nest failure among Hawaiian Ducks. The primary cause of abandonment was not always clear, but 33% of abandoned nests were partially predated. Further, at least 16% of successful nests were partially predated, and one nest was fully predated. On Kauaʻi, rats *Rattus* sp., cats *Felus catus*, pigs *Sus scrofa*, and dogs *Canis lupus familiaris* are thought to be important nest predators (Swedberg 1967; USFWS 2011), and characteristics of predated eggs and nests in this study were consistent with predation by rats and, for one nest, possibly cat (Rearden 1951; Marini & Melo 1998; Fies & Puckett 2000; Sanders & Maloney 2002). The use of nest cameras could help confirm the identity of these suspected nest predators of Hawaiian Duck (Larivière 1999). Non-native mammalian predators can be especially problematic for island endemic, ground-nesting bird species (Milberg & Tyrberg 1993; Burney *et al.* 2001; Blackburn *et al.* 2004) and have been implicated in the decline or extinction of several duck species (*e.g.* Mariana Mallard *Anas oustaleti* and Laysan Duck; Reichel & Lemke 1994; Green 1996; Burney *et al.* 2001; Ferreira & Taylor 2003). Refuge management actions at our study site included control measures for feral cats and rats, and cats were actively trapped during the study period. Our results suggest that the scope of non-native predator control and management actions for the Hawaiian Duck could be expanded from foraging habitat to upland nesting habitat, including forested hillsides and ridges, if managers chose to manage non-native predator impacts on all habitats used by Hawaiian Ducks during nesting.

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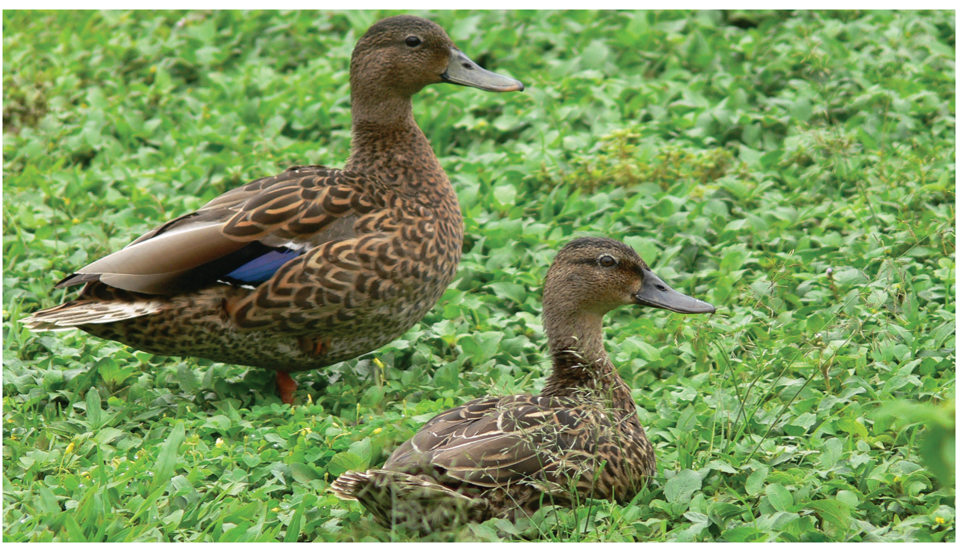

Photograph: Hawaiian Duck pair (left: male; right: female) at Hanalei National Wildlife Refuge, Kaua'i, Hawai'i, USA, by Christopher Malachowski.

