Hawaiian Duck Behavioral Patterns in Seasonal Wetlands and Cultivated Taro

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ABSTRACT An important component for developing effective habitat management plans for the endangered, island-endemic Hawaiian duck (koloa maoli; *Anas wyvilliana*) involves gaining a better understanding of how birds are using habitat and the habitat characteristics that may influence those behaviors. We conducted year-round behavioral and habitat surveys to determine how Hawaiian ducks allocate their time to different activities throughout the annual cycle in managed natural wetlands and wetland taro (*Colocasia esculenta*) agriculture and to evaluate the relative roles provided by these wetland types. We used instantaneous focal sampling ($n = 984$ observation sessions; 328.8 hr) to estimate diurnal time activity budgets and quadrat sampling to characterize wetland habitat features from September 2010 to August 2011 at Hanalei National Wildlife Refuge, Kaua'i, Hawaii, USA. The behavioral activities of birds differed between managed wetlands and taro. Hawaiian ducks spent a greater proportion of time resting (44% vs. 27%) and foraging (15% vs. 11%) when using taro compared to managed wetlands; whereas, birds allocated more time to maintenance (28% vs. 21%), locomotion (22% vs. 7%), and social interactions (1.3% vs. 0.5%) in managed wetlands than taro. Courtship activities accounted for <1% of male Hawaiian duck activity budgets but occurred over 5 times more frequently in managed wetlands (0.6%) than in taro (0.1%). In managed wetlands, birds foraged slightly more with increasing cover of flatsedges (*Cyperus* spp.) and lesser fimbristylis (*Fimbristylis littoralis*), decreasing cover of California grass (*Urochloa mutica*) and Mexican primrose-willow (*Ludwigia octovalvis*), and decreasing water depth. Overall, activity budgets suggest both managed wetlands and taro contribute to fulfilling daily and seasonal resource requirements for Hawaiian ducks. The increased range of activities, particularly courtship and copulation, performed in moist-soil wetlands suggests that greater habitat diversity is provided by seasonal wetland systems. Future research aimed at food production and daily and seasonal patterns of movement and habitat use would expand our understanding of the relative role that taro and managed wetlands provide in meeting the annual habitat needs of Hawaiian duck. © 2018 The Wildlife Society.

KEY WORDS *Anas wyvilliana*, behavior, emergent vegetation, Hawaiian duck, island waterfowl, taro, time-activity budgets, wetland management.

Wetland managers and agricultural producers provide important seasonal wetland habitat for waterfowl and other waterbirds throughout the world (Smith et al. 1989, Hohman et al. 1996, Elphick 2000, Czech and Parsons 2002, Manley et al. 2004). The response of waterfowl to managed seasonal wetlands and agricultural wetlands has been well studied in North America, and habitat management techniques have been refined over decades (Kaminski and Prince 1981, Fredrickson and Taylor 1982, Heitmeyer et al. 1989, Gray et al. 1999, Foster et al. 2010). However, our understanding of bird use of these wetland types is primarily for migrating and wintering waterfowl in temperate regions, and few studies have assessed the relative value of managed moist-soil wetlands and agricultural wetlands for non-migratory, tropical waterfowl (Czech and Parsons 2002, Acosta et al. 2010, Elphick et al. 2010, Sundar and Subramanya 2010).

Because of restricted ranges and lower habitat abundance, non-migratory island-endemic waterfowl must satisfy all of their daily resource requirements (e.g., foraging and roosting habitat) and seasonal life-history requirements (e.g., breeding and molting) within a disproportionately smaller area than their migratory mainland counterparts (Simberloff 1995, Green 1996). Further, some species of tropical or insular anatids may use the same wetland system throughout the annual cycle. Thus, rather than providing resources to complement one specific period of a species' annual cycle (e.g., winter), managers may need to provide habitat for a

variety of waterbird species throughout their entire annual and life cycles at the same time of year (Griffin et al. 1989). Moreover, many of the generalizations related to *Anas* behavior and habitat use that guide seasonal wetland habitat management objectives in temperate and subarctic regions of North America may not necessarily apply to tropical regions and isolated, island systems.

The Hawaiian duck (*Anas wyvilliana*) is the only endemic species of *Anas* extant on the main Hawaiian Islands and currently has the highest recovery priority among the 4 endangered, wetland-dependent birds that occur there (U.S. Fish and Wildlife Service [USFWS] 2011). One objective for Hawaiian duck recovery is to establish a protected and managed network of core and supporting wetlands (USFWS 2011). Hawaiian duck are non-migratory and use a variety of wetland systems that range from low elevation, coastal wetlands to montane streams and bogs (Perkins 1903, Schwartz and Schwartz 1953, Swedberg 1967, Engilis et al. 2002, Uyehara et al. 2008). However, coastal lowland wetlands likely support the highest densities of Hawaiian duck, and the most heavily used lowland wetland types include managed and unmanaged palustrine wetlands and agricultural wetlands used to produce taro (*Colocasia esculenta*). Taro is a traditional Hawaiian food crop and an important staple food in parts of Africa, Pacific island countries, and Asia (Onwueme 1999). Taro on Hawaii is farmed in shallowly flooded fields, or lo'i, similar to rice paddies. Agricultural wetlands in other regions of the world have demonstrated potential to serve as surrogate wetland habitat for waterbirds (Fasola and Ruíz 1996, Elphick 2000, Acosta et al. 2010, Fujioka et al. 2010, Wymenga and Zwarts 2010), but most studies examining waterfowl use of agricultural wetlands have focused on rice and little information exists for other wetlands crops (Czech and Parsons 2002).

Despite the perceived value of managed seasonal wetlands and taro agricultural wetlands to Hawaiian ducks, there is little understanding of how Hawaiian ducks exploit these wetlands to meet their daily and seasonal needs. Several studies have investigated wetland management techniques and agricultural practices in Hawaii (Chang 1990, Rader 2005, Gee 2007, Wirwa 2007, Gutscher-Chutz 2011); however, none have quantified and compared Hawaiian duck use of major land cover types and behavioral response to wetland habitat management and taro cultivation practices. A key component for developing effective habitat management plans for Hawaiian duck involves gaining a better understanding of how birds are using habitat and the habitat characteristics (e.g., water depth, vegetation type, or cover) that may influence those behaviors.

We investigated how Hawaiian ducks allocate their time to different activities in managed natural wetlands and agricultural taro to evaluate the relative roles provided by these wetland types. The specific objectives of this descriptive study were to quantify and compare the time-activity budgets of Hawaiian ducks in managed wetlands and taro, and identify wetland habitat characteristics that influence bird behavior.

STUDY AREA

We conducted our study at Hanalei National Wildlife Refuge (NWR) on the north shore of Kaua'i County, Hawaii (22.204° N, 159.474° W; Fig. 1). The islands of Kaua'i and Ni'ihau supported approximately 90% of remaining Hawaiian ducks (Engilis and Pratt 1993, Engilis et al. 2002), and Hanalei was the single most important low elevation wetland site on those islands (Banko 1987, USFWS 2011). Situated in the floodplain of the lower Hanalei River and surrounded by steep, forested hillsides, the refuge was predominantly flat to gently sloping and generally at 6–12 m above sea level. The 371-ha refuge had 24.4 ha of actively managed moist-soil wetlands, 53.0 ha of cultivated taro lo'i, and 25.8 ha of wetland infrastructure (i.e., ditches and dikes) at the time of our study (Gee 2007, Kaua'i National Wildlife Refuge Complex 2008). The Hanalei River flowed through Hanalei NWR where water was diverted to managed wetlands and taro lo'i. The wetlands were managed as seasonally or semi-permanently flooded palustrine emergent wetlands to benefit the Hawaiian duck and 3 other endangered Hawaiian waterbirds, and as a result, the succession stages and habitat conditions varied between individual impoundments at any given time of year. Taro farming occurred at Hanalei NWR under a special use permit, and approximately two-thirds of annual taro production in the state of Hawaii occurred in the Hanalei region (Cho et al. 2007). Most taro on the refuge had a 12–16-month crop cycle, and planting was staggered throughout the year to allow for year-round harvest. Thus, the taro landscape on the refuge contained a mosaic of cover types that included various age classes of taro, along with wet fallow and dry fallow resting stages that occurred after harvest and before re-planting. Refuge wetlands supported several non-migratory and migratory waterbird species, including listed species such as Hawaiian coot (*Fulica alai*), Hawaiian common gallinule (*Gallinula galeata sandvicensis*), Hawaiian stilt (*Himantopus mexicanus knudseni*), and Hawaiian goose (*Branta sandvicensis*). Mean annual rainfall at Princeville Ranch (1938–2009), 1 km north of Hanalei NWR, was 204 cm/year, allocated between a relatively dry season (May–Oct, 14.7 cm/month) and a wet season (Nov–Apr, 20.0 cm/month; National Climate Data Center, https://www.ncdc.noaa.gov, accessed 01 Aug 2017). Temperatures in this region (1999–2009) fluctuated little throughout the year, and mean low and high temperatures were 19.1°C and 27.8°C, respectively (National Climate Data Center).

METHODS

Behavioral Observations
We selected a representative sample of managed wetlands (*n* = 6) and taro complexes (*n* = 6) from those at Hanalei NWR as focal areas for behavioral observations (Fig. 1). The managed wetland impoundments included a variety of habitat conditions and succession stages, and the taro complexes (33 individual lo'i) spanned a range of taro ages and a diversity of taro farming styles. Wetland impoundments ranged in size from 0.3 to 3.3 ha ($\bar{x}$ = 1.4 ± 1.1 ha [SD]), whereas taro lo'i ranged from 0.1 to 0.5 ha ($\bar{x}$ = 0.2 ± 0.1 ha).
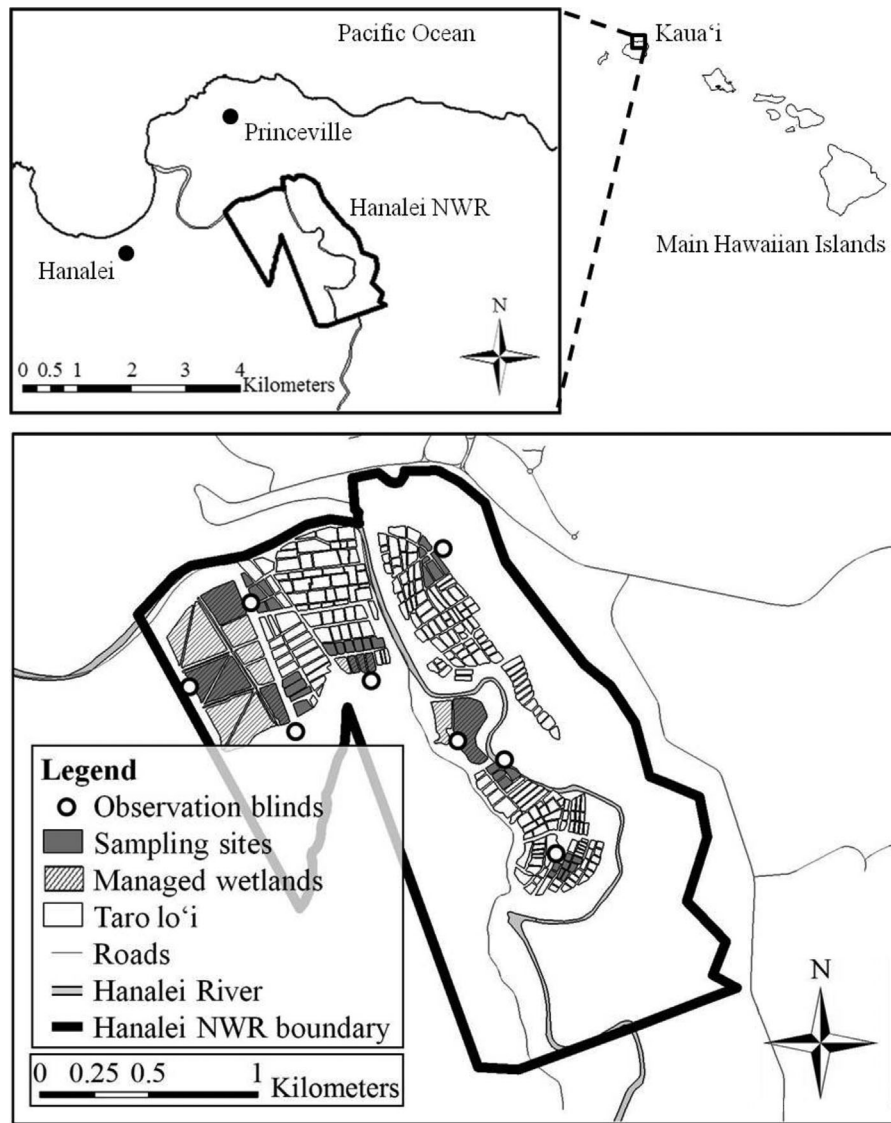
Figure 1. Hawaiian Islands with detail of distribution of managed wetlands and taro lo'i, including sampling sites, at Hanalei National Wildlife Refuge (NWR), Kaua'i, USA, 2010–2011.

We conducted behavioral surveys from 8 3-m-high tower blinds positioned near the study sites. We stratified observation effort by wetland type (managed wetland and taro) and time of day, which we divided into 4 daily periods that spanned from 30 minutes before sunrise to 30 minutes after sunset, to assure representative sampling during daylight hours. We also randomized the order that we visited sites. Within each wetland type, we recorded if individuals were in the unit or on a dike. Within taro, we further categorized cover classes as taro (included planting through harvest phase of the crop cycle), wet fallow, and dry fallow. Fallow lo'i either contained predominantly non-taro emergent vegetation or lacked vegetative cover. To minimize the chance of recording observer-influenced behavior, we waited ≥5 minutes after arriving at survey sites before beginning behavior surveys.

We randomly selected focal individuals for behavioral sampling by counting the number of Hawaiian ducks (i) at the survey site, obtaining a random number (j) from a random number chart, and counting birds left to right until we reached the jth individual. We determined the sex and age (juvenile, adult) of each focal individual using plumage characteristics (A. E. Engilis Jr., University of California-Davis, unpublished data). Because we were not always able to discern birds in formative and first alternate plumage (i.e., first year birds) from birds in definitive basic and alternate plumage, we grouped these birds with adults. We recorded pair status of focal individuals at the end of each observation session using criteria described by Paulus (1983). We did not conduct focal observation on ducklings; however, we sampled females with broods.

We used instantaneous focal sampling procedures (Altmann 1974) to quantify the time-activity budgets of Hawaiian ducks from September 2010 through August 2011. We observed birds with a 20–60× spotting scope or 10× binoculars, and we recorded the behavioral activity of focal individuals at 10-second sample intervals for up to 30 minutes using a digital voice-activated recorder and

electronic timer (Baldassarre et al. 1988, Dugger and Petrie 2000). Given the Hawaiian duck is closely related to the mallard (*Anas platyrhynchos*), we adopted behavior terminology for mallards (Lorenz 1951, Johnsgard 1965, McKinney 1965). We assigned behaviors to 73 distinct activities (Malachowski 2013); however, for most analyses, we grouped behaviors into 6 general behavioral categories: foraging, resting, maintenance, locomotion, alert, and social (includes courtship, intraspecific agonistic interactions, and interspecific agonistic interactions). We further classified foraging behaviors as dabble, head-dip, up-end, probe, nibble vegetation, peck, snatch or snap, and other. We recorded instantaneous behaviors as events and states, where events were instantaneous occurrences of a behavior, and states occurred in a continuum (Altmann 1974). We combined behavioral states and events to determine the total proportion of time for each behavior.

When focal birds moved out of sight, we recorded behavior as out of view until the individual returned into view. If the focal individual remained out of view, left the survey site, or switched cover types, and if a bird of similar sex, age, and pair status was present in the same wetland type and cover class at the survey site, we continued the observation session by watching the alternate bird (Losito et al. 1989); otherwise, the session would end. We recorded anthropogenic disturbances that altered the behavior of focal individuals and the primary response to the disturbance as alert, take cover, or flush. To maximize the independence of behavioral responses among focal samples, we conducted no more than one behavioral observation session per survey site per time period in a given day, and most (94%) observation sessions at a given survey site were separated by ≥ 1 day. We used observation sessions lasting between 5 and 30 minutes ($\bar{x} = 20.0 \pm 7.9$ min) for subsequent analyses to minimize biasing samples towards more sedentary behaviors that may occur more frequently in longer sessions or more active behaviors that may occur during shorter sessions. One observer collected all data to eliminate inter-observer variation.

Sampling Wetland Vegetation and Water Depth

We used quadrat sampling procedures to characterize habitat features within each of the 6 managed wetland units selected for behavioral sampling at Hanalei NWR. We randomly selected 30 sampling points for each managed wetland. To generate sampling points within each site, we used a handheld global positioning system (GPS) unit to record the perimeter of the sampling site and used ArcGIS, version 9.3 (ESRI, Redlands, CA, USA) to randomly select 30 points separated by >2 m. We uploaded the resultant sampling points into a GPS unit (accuracy ≤ 4.0 m), located each site in the field, and marked each sampling point with a pin flag. We then used a random number generator to select the angle at which we positioned each 1.0×0.5-m quadrat on the sampling point.

At each sampling point, we measured water depth at the pin flag. Within each quadrat, we measured maximum vegetation height, and we visually estimated total vegetation cover, vegetation cover by species, and percent of open water area (including open water area in the subcanopy [i.e., below shrub or emergent plant cover]). We sampled wetlands in

September and October 2010 and then every other month through August 2011. During each sampling session, we returned to the same sampling point locations and used the same randomly selected bearings to orient the quadrat. If we could not relocate pin flags (4% of samples), we used a GPS unit to relocate and remark the sampling point. We summarized bi-monthly sampling data within each wetland sampling site by calculating the means of each habitat variable, and we applied these mean habitat characteristic values to dates ranging between the midpoints of preceding and succeeding sampling occasions.

Statistical Analyses

Prior to analyses, we converted activity data to proportions of time engaged in each behavior during each focal observation session (Baldassarre et al. 1988). We used individual focal observation sessions as the sample unit to determine the relationship between dependent variables (i.e., proportion of time engaged in each behavioral state) and wetland type (moist soil wetland and taro). Because individual behaviors in a focal observation sample were not independent (i.e., the proportion of time spent in one behavioral activity affects the proportion of time spent in other activities), we used factorial multivariate analysis of variance (MANOVA) using Wilks' lambda test criterion to simultaneously evaluate the effect of wetland type on time-activity budgets after accounting for pair status, age, and month (Ramsey and Schafer 2002). We included a sex-wetland type interaction term to test if behavioral patterns differed between wetland types by sexes. We removed age from subsequent models because primary behavioral activities did not differ between juveniles ($n = 95$) and adults ($n = 807$; MANOVA; Wilks' $\lambda = 0.99$, $F_{6,879} = 0.85$, $P = 0.53$).

If MANOVA indicated significant effects of wetland type or a sex-wetland type interaction ($P < 0.05$), we used univariate analysis of variance (ANOVA) to further examine the effects on separate behaviors. We applied logit transformations to proportions values prior to analysis to improve homogeneity of variances and meet the assumption of normality for the residuals of the linear models (Ramsey and Schafer 2002). If logit transformations failed to normalize the residuals and satisfy the equal variance assumption for parametric testing, we used the Kruskal–Wallis test to compare the untransformed proportion of time engaged in the activity between explanatory variables (Ramsey and Schafer 2002). We also used the Kruskal–Wallis test to evaluate the effects of explanatory variables on specific foraging and social behaviors (courtship and display). For all procedures, we adjusted P-values for each family of *a priori* comparison tests using the Benjamini–Hochberg method to control the false discovery rate at 5% (Benjamini and Hochberg 1995).

We used Spearman's correlation analysis to assess associations between behavioral activities and managed wetland habitat characteristics. In addition, we tested the relationship between foraging activity and proportion of cover by 6 plant species that were the focus of management actions and thought to be beneficial (flatsedges [*Cyperus* spp.], barnyard grass [*Echinochloa crus-galli*], lesser fimbristylis [*Fimbristylis littoralis*], Mexican primrose-willow [*Ludwigia*

octovalvis]) or detrimental (Vasey's grass [*Paspalum urvillei*], California grass [*Urochloa mutica*]) for Hawaiian ducks and wetlands by habitat managers (Smith 2011). We used a 1-sided Fisher's exact test (Ramsey and Schafer 2002) to assess if the proportion of focal samples involving anthropogenic disturbances differed between wetland types; specifically, we tested the prediction that disturbances occurred more frequently in taro than managed wetlands since lo'i are generally smaller than wetland units, which may make disturbances more difficult to avoid. All time-activity budget values are reported as untransformed means ± standard error (SE).

RESULTS

Between September 2010 and August 2011, we collected 984 focal samples from 224 females ($n_{\text{female, managed wetland}} = 104$, $n_{\text{female, taro}} = 120$) and 760 males ($n_{\text{male, managed wetland}} = 388$, $n_{\text{male, taro}} = 372$) over 328.8 hours of observation. The distribution of the sample between sexes was consistent with the sex ratio of birds at Hanalei NWR (C. P. Malachowski, Oregon State University, unpublished data). Overall, Hawaiian ducks spent the most time resting ($35.6 \pm 1.1\%$), followed by maintenance ($24.8 \pm 0.8\%$), locomotion ($14.7 \pm 0.6\%$), foraging ($13.1 \pm 0.8\%$), alert ($11.0 \pm 0.4\%$), and social interactions ($0.9 \pm 0.1\%$).

Behavioral activities of Hawaiian ducks differed between managed wetlands and taro (MANOVA; Wilks' $\lambda = 0.84$, $F_{6,962} = 30.5$, $P < 0.001$); however, the nature of those differences depended on sex (wetland type × sex: Wilks' $\lambda = 0.97$, $F_{6,962} = 4.53$, $P < 0.001$). Behavior patterns of female Hawaiian ducks did not differ between wetland types, except for locomotion, which occurred more often in managed wetlands (14.0%) than in taro (6.7%; Table 1).

For males, the effect of wetland type was significant for all behavioral categories except alert behavior. Although the difference was small, male Hawaiian ducks spent a greater proportion of time foraging when using taro (13.3%) than when using managed wetlands (10.3%). In addition, males allocated more time to resting when using taro than managed wetlands (45.5% vs. 25.0%), whereas birds allotted more time to maintenance and locomotion in managed wetlands than taro (28.4% vs. 20.4% and 24.1% vs. 7.7%, respectively). The proportion of time engaged in social behaviors by males was generally low but higher in managed wetlands (1.5%) than in taro (0.6%). More specifically, courtship occurred more frequently in managed wetlands ($0.6 \pm 0.1\%$) than in taro ($0.1 \pm 0.05\%$; Kruskal-Wallis, $H_1 = 24.3$, $P < 0.001$), and copulation, which occurred in 1.4% of observation sessions in managed wetlands, was not observed in any samples in taro.

The primary foraging tactics used by Hawaiian ducks were head-dipping and dabbling; however, birds allocated foraging tactics differently between managed wetlands and taro (MANOVA; Wilks' $\lambda = 0.97$, $F_{8,961} = 3.33$, $P < 0.001$; Table 2). Probing in mud and matted vegetation constituted a larger proportion of foraging behavior within managed wetlands than taro, whereas birds spent more foraging time head-dipping in taro.

Within taro the behavioral activities of Hawaiian ducks differed significantly between birds in lo'i and on dikes (MANOVA; Wilks' $\lambda = 0.34$, $F_{6,470} = 149.7$, $P < 0.001$; Table 3). Hawaiian ducks used taro lo'i dikes for resting (60.0%), whereas birds entered lo'i primarily to forage (44.8%). Activity budgets of Hawaiian ducks also differed among taro cover classes, excluding samples on dikes (MANOVA; Wilks' $\lambda = 0.80$, $F_{12,278} = 2.67$, $P = 0.002$). Birds spent the greatest percentage of time foraging in taro

Table 1. Comparisons of the percent time ($\bar{x} \pm$ SE) that female and male Hawaiian ducks spent in 6 behavioral categories in managed wetlands ($n = 492$ observation sessions) and taro lo'i ($n = 492$) at Hanalei National Wildlife Refuge, Kaua'i, USA from September 2010 to August 2011.

Sex	Behavior	Managed wetland		Taro lo'i		Test statistic value[a]	P-value
		$\bar{x}$	SE	$\bar{x}$	SE		
Female	Forage	14.2	2.5	20.4	3.1	0.71[KW]	0.400
	Rest	33.7	3.2	40.6	3.4	0.39	0.534
	Maintenance	27.9	2.6	24.1	2.6	1.88	0.171
	Locomotion	14.0	1.6	6.7	0.8	18.43	<0.001
	Alert	9.5	1.2	7.9	0.8	2.01	0.158
	Social	0.5	0.1	0.3	0.1	1.66[KW]	0.198
	n	104		120			
Male	Forage	10.3	1.1	13.3	1.4	4.24[KW]	0.039
	Rest	25.0	1.6	45.5	1.8	65.88	<0.001
	Maintenance	28.4	1.4	20.4	1.1	18.89	<0.001
	Locomotion	24.1	1.3	7.7	0.5	134.02	<0.001
	Alert	10.8	0.7	12.5	0.7	2.52	0.113
	Social	1.5	0.2	0.6	0.1	9.79[KW]	0.002
	n	388		372			
Overall	Forage	11.1	1.0	15.0	1.3	4.59[KW]	0.032
	Rest	26.8	1.4	44.3	1.6	54.63	<0.001
	Maintenance	28.3	1.2	21.3	1.0	20.31	<0.001
	Locomotion	22.0	1.1	7.5	0.4	147.37	<0.001
	Alert	10.6	0.6	11.4	0.6	0.65	0.421
	Social	1.3	0.2	0.5	0.1	11.88[KW]	<0.001
	n	492		492			

[a] Test statistics are *F*-values from separate analyses of variance after accounting for pair status and month unless otherwise indicated; [KW] = Kruskal-Wallis *H*-values.

Table 2. Relative frequency of occurrence (%) of foraging behaviors exhibited by Hawaiian ducks using managed wetlands ($n = 205$ observation sessions; 17.5 hr) and taro loʻi ($n = 151$; 23.4 hr) at Hanalei National Wildlife Refuge, Kauaʻi, USA from September 2010 to August 2011. Behaviors occurring less than 1.0% of the time were listed as trace (tr).

	Relative frequency of occurrence (%) of foraging behaviors		
Foraging behavior	Managed wetlands	Taro loʻi	Overall
Dabble	30.8	33.7	32.5
Head-dip	46.2	59.2	53.6
Up-end	2.9	tr	1.4
Probe	14.6	4.0	8.5
Nibble vegetation	4.5	1.5	2.8
Other[a]	1.0	1.2	1.1

[a] Includes pecking and snatching.

(51.0%) and wet fallow (40.0%) and the least in dry fallow (27.8%; Table 4). Conversely, birds spent more time resting when using dry fallow compared to other cover classes. Behavior patterns on dikes versus in loʻi and among taro cover classes did not differ between sexes ($P > 0.2$).

Water depth, species-specific emergent wetland plant cover, total vegetative cover, and vegetation height varied within each of the 6 sampled managed wetland units throughout the year. Mean water depth across units was 11.1 ± 1.3 cm but ranged from 0 to 43.9 cm. We identified 41 unique plant species in managed wetlands, including 7 (17.1%) that were indigenous to Hawaii (Appendix A; Wagner et al. 2005). Mean species richness per impoundment per sampling period was 12.2 ± 0.8, and mean species richness per impoundment (across months) was 21.0 ± 2.0. Mean vegetative cover was $43.5 \pm 3.1\%$, but cover ranged from less than 1% in recently treated, early successional wetlands to 77.8% in mid-late successional wetlands. There were no strong associations between wetland habitat characteristics and foraging effort ($|r_s| \leq 0.23$). Foraging behavior was negatively correlated with mean emergent vegetation height ($r_s = -0.18$, $P < 0.001$) and mean water depth ($r_s = -0.12$, $P = 0.016$). Also, Hawaiian ducks foraged slightly more with increasing cover of flatsedges

Table 3. Comparison of time-activity budgets ($\bar{x} \pm$ SE) of Hawaiian ducks in taro loʻi ($n = 163$ observation sessions) and on taro loʻi dikes ($n = 329$) at Hanalei National Wildlife Refuge, Kauaʻi, USA from September 2010 to August 2011.

	Percent time spent per behavior					
	In taro loʻi		On taro dike			
Behavior	$\bar{x}$	SE	$\bar{x}$	SE	Test statistic value[a]	P-value
Forage	44.8	2.7	0.3	0.1	302.38[KW]	<0.001
Rest	12.7	1.9	60.0	1.6	377.25	<0.001
Maintenance	21.6	2.0	21.1	1.2	0.39	0.535
Locomotion	12.7	0.9	4.9	0.4	89.24	<0.001
Alert	7.5	0.6	13.3	0.8	11.48	<0.001
Social	0.6	0.1	0.4	0.1	0.04[KW]	0.836

[a] Test statistics are F-values from separate analyses of variance after accounting for sex, pair status, and month unless otherwise indicated; [KW] = Kruskal-Wallis H-values.

($r_s = 0.18$, $P < 0.001$) and lesser fimbristylis ($r_s = 0.17$, $P = 0.001$) and with decreasing cover of California grass ($r_s = -0.15$, $P = 0.003$) and Mexican primrose-willow ($r_s = -0.23$, $P < 0.001$).

The proportion of observation sessions with ≥ 1 human-related disturbance to Hawaiian ducks was greater in taro (14.0%) than managed wetlands (10.4%; Fisher's exact test, $P = 0.049$). Disturbances most frequently involved taro farmers and USFWS personnel, accounting for 43.4% and 32.6% of all disturbance events, respectively. Other disturbances included planes and helicopters (14.0%), public (5.4%), and sirens (4.7%). Most human-related disturbances (71.3%) elicited a low-intensity response (i.e., alert behavior) and the remainder of disturbances resulted in high-intensity (21.7%; i.e., flush) or mid-intensity (7.0%; i.e., take cover) responses.

DISCUSSION

Hawaiian ducks allocated diurnal activity budgets differently in managed and cultivated wetland habitat at Hanalei NWR. Although the differences in behavior between wetland types depended on sex, the patterns were similar for male and females. In general, birds used taro loʻi and dikes primarily for resting and foraging, whereas birds used managed wetlands for maintenance, rest, food, courtship, and copulation. The lower proportion of time spent resting in managed wetlands was largely offset by more time locomoting, which may relate to the larger size of wetland impoundments compared to taro loʻi. More evenly distributed activities and the occurrence of more mating behavior in managed wetlands may reflect the greater habitat diversity provided by moist-soil wetlands including vegetation structure, patchiness, emergent wetland plant species richness, and range of water depths. Consistent with this pattern, Hawaiian ducks employed a more diverse suite of foraging tactics in managed wetlands. Although birds spent slightly more time foraging when using taro, the difference equates to about 30 minutes during a regular 12-hour day, which seems of minimal biological consequence given the percent of time that birds allocated to feeding each day is generally low. It is possible that birds use wetland types differently at night, and Hawaiian ducks can be active at night (B. D. Dugger, Oregon State University, personal observation); however, our sampling efforts were restricted to crepuscular and diurnal hours, and the extent of such nocturnal activity is unknown.

Hawaiian ducks spent more time foraging in managed wetland units that contained more lesser fimbristylis and flatsedge cover, although the relationship was weak. Lesser fimbristylis was common in most wetland units, but cover was highest in early successional wetlands. These moist-soil plant species provide high seed production and important nutrient sources (e.g., carbohydrates and protein; DesRochers et al. 2009, 2010), and they are among the species targeted by wetland management at Hanalei NWR (C. C. Smith, USFWS, personal communication). We observed birds dabbling seeds (e.g., Mexican primrose-willow, flatsedges) from the water surface and nibbling the seeds, leaves, and

Table 4. Comparisons of the percent time ($\bar{x} \pm$ SE) that Hawaiian ducks spent in 6 behavioral categories in 3 taro cover classes ($n = 163$ observation sessions) at Hanalei National Wildlife Refuge, Kaua'i, USA from September 2010 to August 2011. Multiple comparison tests with a Benjamini–Hochberg correction indicate significant differences ($P < 0.05$) between cover classes with superscripts (T = taro, WF = wet fallow, DF = dry fallow); superscripts in parentheses represent marginally significant differences ($0.05 \leq P < 0.10$).

| | Taro cover classes | | | | | | | |
| | Taro | | Wet fallow | | Dry fallow | | | |
Behavior	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Test statistic value[a]	P-value
Forage	51.0	3.6[DF, (WF)]	40.0	4.3[(T)]	27.8	10.0[T]	8.51[KW]	0.014
Rest	9.6	2.1[DF]	10.0	2.6[DF]	44.1	10.4[T,WF]	8.50[KW]	0.014
Maintenance	20.5	2.7	24.2	3.4	16.7	5.2	0.08	0.919
Locomotion	11.9	1.2[DF, (WF)]	15.9	1.7[DF, (T)]	3.8	1.1[T,WF]	15.17[KW]	<0.001
Alert	6.1	0.7[(WF)]	9.4	1.1[(T)]	7.5	2.2	4.51[KW]	0.105
Social	0.8	0.2	0.5	0.2	tr		3.87[KW]	0.144
n	87		62		14			

[a] Test statistics are F-values from separate analyses of variance after accounting for sex, pair status, and month unless otherwise indicated; [KW] = Kruskal-Wallis H-values.

inflorescences of vegetation, including Mexican primrose-willow, Javanese flatsedge (*Cyperus javanicus*), manyspike flatsedge (*Cyperus polystachyos*), lesser fimbristylis, forked fimbry (*Fimbristylis dichotoma*), rock bulrush (*Schoenoplectus juncoides*), barnyard grass, and crowngrasses (*Paspalum* spp.). A relatively common form of this foraging behavior involved stripping or breaking the seed pods of Mexican primrose-willow and dabbling the released seeds off the surface of the water column. In addition, wetlands plants such as lesser fimbristylis and barnyard grass provide important structure and nutrients for aquatic invertebrates (Smock and Stoneburner 1980, Magee 1993), which may be a valuable source of proteins and lipids for ducks (Voigts 1976, Fredrickson and Taylor 1982, Batzer and Resh 1992). Close visual observations of foraging behavior revealed that birds probing in matted vegetation, particularly lesser fimbristylis, and soil, occasionally extracted invertebrates, such as snails (Gastropoda) and worms (Oligochaeta). During draw-down periods in both wetland types, we occasionally observed birds head-dipping in a rapid, sweeping motion and surfacing with tadpoles and possibly fish.

Courtship activities accounted for <1% of male Hawaiian duck activity budgets but occurred over 5 times more frequently in managed wetlands (0.6%) than in taro (0.1%). Further, copulation occurred in 1.4% of observation sessions in managed wetlands but was not observed in any samples in taro. Data on courtship habitat requirements are rare for anatids; however, habitat conditions that provide a safe and undisturbed setting for courtship may have implications for pair formation and recruitment and may, therefore, be an important consideration for managers. Closely related species, such as mallard and mottled duck (*Anas fulvigula*), often use shrub-scrub wetlands or small pockets of open water surrounded by dense vegetation for courtship, as these land cover types may provide greater protection from predators (Weeks 1969, Heitmeyer 1985). Miller (1985) reported that northern pintail (*Anas acuta*) wintering in California allocated more time to courtship in marshes than agricultural wetlands (flooded rice fields) and suggested that the difference was due to larger flocks associated with larger wetlands. Wetland units at Hanalei NWR were generally

larger than taro lo'i and had a hemi-marsh structure where pockets of open water were interspersed amongst emergent wetland vegetation, which may provide cover from avian predators and human-related disturbances, and visual isolation from conspecifics.

Hawaiian ducks used taro predominantly for resting and foraging. We frequently observed birds resting on the dikes of taro lo'i that crisscross the Hanalei NWR landscape. Similar to previous surveys (Gee 2007, Gutscher-Chutz 2011), most Hawaiian ducks were on dikes as opposed to in lo'i, and birds spent 60% of the time loafing when on taro dikes. Taro dikes are elevated and often provide good visibility, which possibly aids in predator detection, and quick access to escape cover. Among taro cover classes, Hawaiian ducks allocated the greatest proportion of time to foraging when using lo'i containing taro; however, foraging time was relatively high for all cover classes. Taro provides benefits to waterbirds in the form of cover and production of aquatic invertebrates (Gutscher-Chutz 2011), including taxa reported in the diet of Hawaiian duck (Henshaw 1902, Perkins 1903, Munro 1944, Schwartz and Schwartz 1953, Engilis et al. 2002). We observed Hawaiian ducks feeding on filamentous green algae (Chlorophyceae), lesser duckweed (*Lemna aequinoctialis*), and large mosquito fern (*Azolla filiculoides*), species that were abundant in many lo'i and possibly linked to large nutrient influxes associated with fertilizer applications. Birds also nibbled and probed at the base of taro plants, and foraged in and around post-harvest waste taro. In less intensively managed taro lo'i and fallow lo'i where non-taro emergent vegetation (e.g., rock bulrush, Mexican primrose-willow) was present, birds engaged in foraging behaviors similar to those used in managed wetlands (C. P. Malachowski, Oregon State University, personal observation).

Few studies have directly compared waterfowl use of agricultural wetlands and natural wetlands, and most work has focused on rice (Czech and Parsons 2002, Elphick et al. 2010). The proportion of time spent foraging by Hawaiian ducks in taro (15%) falls within the lower range of estimates of time allocated to diurnal feeding in flooded rice fields by Holarctic dabbling ducks such as northern pintail (~6–35%; Miller 1985, Rave and Cordes 1993). Studies reported that

continental waterfowl (e.g., northern pintail, lesser snow geese [*Chen caerulescens caerulescens*]) spent more time foraging in natural marshes than rice fields, and although speculative, they attributed the difference to greater foraging efficiency (i.e., higher metabolizable energy intake rate and lower foraging effort) of birds using rice (Miller 1985, Jonsson and Afton 2006). Hawaiian ducks exhibited the opposite pattern (i.e., greater foraging in taro vs. natural wetlands), which may suggest that birds are able to feed more efficiently in managed wetlands. Habitat-specific estimates of Hawaiian duck diet and feeding efficiency, along with estimates of food diversity and biomass, would help guide our interpretation of observations on foraging behavior.

Consistent with our prediction, Hawaiian ducks were disturbed less often in managed wetlands than taro; however, the difference in human-related disturbances between wetland types was comparatively small (10% vs. 14%) and of questionable biological significance. The mean patch size of both wetland types in our study was considerably smaller than for wetlands used in similar studies on the mainland; thus, we might expect overall disturbance to be higher in Hawaii, but that does not appear to be the case. Disturbances in our study occurred at a rate of approximately 0.5 events/hour, which is within the bounds of anthropogenic disturbance rates reported for waterfowl in North America and Europe (0.1–1.0 disturbances/hr; Bélanger and Bédard 1989, Morton et al. 1989, Havera et al. 1992, Riddington et al. 1996, Ladin et al. 2011). In several of the comparison studies, disturbances were defined as events that elicited a flight response. If we apply that criteria to our data, disturbances occurred at a rate of 0.1 events/hour, which is at the lower range of rates reported for other waterfowl species in other regions of the world. This lower disturbance rate may be associated with residency by some Hawaiian ducks and acclimation to farming and refuge activities, or with smaller flock sizes (Hawaiian ducks most frequently observed singly or in pairs; Malachowski 2013), which tend to be less wary and more tolerant of disturbance than larger flocks (Owens 1977, Bélanger and Bédard 1989, Riddington et al. 1996).

MANAGEMENT IMPLICATIONS

Habitat management plans at Hanalei NWR aim to provide a suite of habitat conditions for multiple life-history stages of endangered Hawaiian waterbirds at any given time. Activity budgets suggest that managed wetlands and taro contribute to fulfilling daily and seasonal resource requirements for Hawaiian ducks. The increased range of activities, particularly courtship and copulation, performed in moist-soil wetlands suggests that wetlands meet a broader range of habitat requirements than taro. Habitat conditions that are favorable to courtship behavior may be important for pair formation and recruitment. In addition, our results support management objectives to target flatsedge and lesser fimbristylis as forage for Hawaiian ducks. A more complete understanding of the relative role that taro and managed wetlands provide in meeting the annual habitat needs of Hawaiian ducks would benefit from studies that estimate food production and daily and seasonal patterns of movement and habitat use.

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APPENDIX A

Plant species occurring in managed natural wetlands at Hanalei National Wildlife Refuge, Kaua'i, USA between September 2010 and August 2011. Scientific names and growth habits of plant species based on the United States Department of Agriculture PLANTS database (U.S. Department of Agriculture 2017). Native status categories include indigenous (N) and introduced or naturalized (I; Wagner et al. 2005).

Family	Common name	Scientific name	Native status	Growth habit
Alismataceae	Broadleaf arrowhead	*Sagittaria latifolia*	I	Forb or herb
Apiaceae	Asiatic pennywort	*Centella asiatica*	I	Forb, herb, or subshrub
Asteraceae	Bluemink	*Ageratum houstonianum*	I	Forb or herb
	False daisy	*Eclipta prostrata*	I	Forb or herb
	Florida tasselflower	*Emilia fosbergii*	I	Forb or herb
	Wedelia	*Sphagneticola trilobata*	I	Forb or herb
Caryophyllaceae	Whitesnow	*Drymaria cordata* var. *pacifica*	I	Forb or herb
Commelinaceae	Climbing dayflower	*Commelina diffusa*	I	Forb or herb
Convolvulaceae	Littlebell	*Ipomoea triloba*	I	Forb, herb, or vine
Cyperaceae	Variable flatsedge	*Cyperus difformis*	I	Sedge
	Javanese flatsedge	*Cyperus javanicus*	N	Sedge
	Fragrant flatsedge	*Cyperus odoratus*	N	Sedge
	Fuzzy flatsedge	*Cyperus pilosus*	I	Sedge
	Manyspike flatsedge	*Cyperus polystachyos*	N	Sedge
	Forked fimbry	*Fimbristylis dichotoma*	N	Sedge
	Lesser fimbristylis	*Fimbristylis littoralis*	I	Sedge
	Shortleaf spikesedge	*Kyllinga brevifolia*	I	Sedge
	Rock bulrush	*Schoenoplectus juncoides*	N	Sedge
Euphorbiaceae	Niruri	*Phyllanthus debilis*	I	Forb or herb
Fabaceae	Threeflower ticktrefoil	*Desmodium triflorum*	I	Forb or herb
	Wild bushbean	*Macroptilium lathyroides*	I	Forb, herb, or vine
	Shameplant	*Mimosa pudica* var. *unijuga*	I	Forb or herb
Lythraceae	Valley redstem	*Ammannia coccinea*	I	Forb, herb, or subshrub
Lythraceae	Colombian waxweed	*Cuphea carthagenensis*	I	Forb or herb
Myrsinaceae	Shoebutton	*Ardisia elliptica*	I	Shrub or tree
Onagraceae	Mexican primrose-willow	*Ludwigia octovalvis*	N	Forb, herb, or subshrub
	Marsh seedbox	*Ludwigia palustris*	I	Forb or herb
Poaceae	Barbas de indio	*Andropogon bicornis*	I	Grass
	Job's tears	*Coix lacryma-jobi*	I	Grass
	Barnyard grass	*Echinochloa crus-galli*	I	Grass
	Guinea grass	*Megathyrsus maximus*	I	Grass
	Hilo grass	*Paspalum conjugatum*	I	Grass
	Panama crowngrass	*Paspalum fimbriatum*	I	Grass
	Kodo millet	*Paspalum scrobiculatum*	N	Grass
	Vasey's grass	*Paspalum urvillei*	I	Grass
	Seashore paspalum	*Paspalum vaginatum*	I	Grass
	Glenwood grass	*Sacciolepis indica*	I	Grass
	Bristle grass	*Setaria* spp.	I	Grass
	California grass	*Urochloa mutica*	I	Grass
Pteridaceae	Water sprite	*Ceratopteris thalictroides*	I	Forb or herb
Rubiaceae	Woodland false buttonweed	*Spermacoce assurgens*	I	Forb, herb, or subshrub