AN ABSTRACT OF THE THESIS OF

Christopher P. Malachowski for the degree of Master of Science in Wildlife Sciences presented on July 25, 2013.
Title: Hawaiian Duck (*Anas wyvilliana*) Behavior and Response to Wetland Habitat Management at Hanalei National Wildlife Refuge on Kaua'i.

Abstract approved:

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Bruce D. Dugger

The endangered Hawaiian Duck (koloa maoli; *Anas wyvilliana*), a non-migratory and island-endemic species, experienced a significant population decline during the twentieth century due to factors such as habitat loss, overharvest, introduced mammalian predators, and hybridization with introduced feral Mallards (*A. platyrhynchos*). A key objective for Hawaiian Duck recovery is to establish a protected and managed network of wetland habitats; however, development of effective habitat management plans is stymied by the lack of information on patterns of habitat use in relation to fundamental resource requirements. Furthermore, many generalizations regarding dabbling duck behavior and resource requirements that guide seasonal wetland management objectives in North America may not apply to tropical regions and island systems. In this thesis, I compare the behavioral repertoire of the Hawaiian Duck with closely related island-endemic waterfowl and migratory North American *Anas*, I investigate the behavioral response of Hawaiian Ducks to wetland habitat management and taro cultivation, and I examine the effects of environmental, climatic, temporal, and social factors on the activity budgets of Hawaiian Ducks.

I conducted instantaneous focal sampling (*n* = 984 observation sessions; 328.8 hr) throughout the annual cycle from September 2010 to August 2011 at managed wetlands and taro lo'i within Hanalei National Wildlife Refuge (NWR), Kaua'i. I documented 73 specific Hawaiian Duck behaviors in eight broad behavior categories including foraging, maintenance, resting, locomotion, alert, courtship, and intraspecific and interspecific agonistic interactions. I found that the behavioral repertoire of the Hawaiian Duck was

similar to that of the Mallard; however, subtle variations in the form and linkage of certain courtship displays, such as nod-swimming, were observed. Additionally, male Hawaiian Ducks were occasionally associated with brood-rearing females (11% of brood observations), and this behavior appeared to be a male strategy whereby females received little perceived benefit , but males may have potentially garnered additional breeding attempts or maintained pair-bonds for subsequent breeding seasons.

After accounting for sex, pair status, month, and time of day, the diurnal behavioral activities of Hawaiian Ducks differed between managed wetlands and taro habitats ($F_{6,960} = 30.3$, $P < 0.001$). Hawaiian Ducks utilized taro predominantly for resting (44%), maintenance (21%), and foraging (15%), while birds used managed wetlands for a variety of activities, including foraging (11%), maintenance (28%), resting (27%), and locomotion (22%). Social activities, particularly courtship, occurred more frequently in managed wetlands than in taro ($H_1 = 11.9$, $P < 0.001$). In managed wetlands, birds foraged slightly more with increasing cover of *Cyperus* spp. ($r = 0.18$, $P < 0.001$) and *Fimbristylis littoralis* ($r = 0.17$, $P < 0.01$) and decreasing cover of *Urochloa mutica* ($r = -0.15$, $P < 0.01$) and wetland vegetation height ($r = -0.22$, $P < 0.001$). Within taro habitat, the behavioral activities of Hawaiian Ducks differed significantly between birds in loʻi and on dikes ($F_{6,468} = 142.8$, $P < 0.001$); birds utilized loʻi dikes for resting (60%) and maintenance activities (21%), whereas birds entered loʻi primarily to forage (45%).

The activity budget of Hawaiian Ducks was strongly influenced by time of day ($F_{18,2715.78} = 6.4$, $P < 0.001$), and birds spent more time engaged in active behaviors (i.e., foraging, locomotion, and alert) and less time resting during early morning and evening than during late morning and afternoon. While strong seasonal shifts in most behavioral patterns were not detected, males allocated more time to courting (1.1 vs. 0.3%; $H_1 = 6.92$, $P = 0.009$) and mate-guarding (0.5 vs. <0.1%; $H_1 = 9.83$, $P = 0.002$) in managed wetlands between November and March than the remainder of the year. The effects of sex ($F_{6,960} = 6.06$, $P < 0.001$) and social status ($F_{6,682} = 6.69$, $P < 0.001$) on activity budgets were also significant. Females spent more time foraging (18 vs. 12%) and less time in alert, locomotor, and social behaviors than males. Paired birds allocated more

time to aggression towards conspecifics, mate-guarding, and courtship, and within taro lo'i, paired birds foraged more and rested less than unpaired birds.

Overall, Hawaiian Duck allocated diurnal activity budgets differently in managed and cultivated wetland habitat at Hanalei NWR, suggesting that both systems may play an important role in fulfilling fundamental daily and seasonal resource requirements. The increased range of activities and foraging tactics used in managed wetlands may indicate the greater habitat diversity (e.g., vegetation structure, patchiness, plant species richness, range of water depths) provided by seasonal wetlands. In general, Hawaiian Duck allocated less time to diurnal foraging than North American *Anas*, such Mallard and Mottled Duck (*A. fulvigula*), suggesting that Hawaiian Duck may have lower daily and seasonal energy demands, have access to higher quality diet, or allot more time to nocturnal foraging activities. Also, unlike many North American migratory waterfowl that demonstrate significant behavioral plasticity in adjusting activity budgets to meet seasonal energy demands associated with breeding, molting, wintering, and migration, Hawaiian Duck did not exhibit a strong seasonal shift in most behaviors which may reflect their non-migratory nature and asynchronous life history cycle.

Hawaiian Duck (*Anas wyvilliana*) Behavior and Response to Wetland Habitat
Management at Hanalei National Wildlife Refuge on Kaua'i

by
Christopher P. Malachowski

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Christopher P. Malachowski, Author

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CONTRIBUTION OF AUTHORS

Dr. Bruce Dugger acquired funding and assisted with all aspects of this research project.

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INTRODUCTION

Quantifying how birds allocate time to various activities on a daily and seasonal basis provides insight into how they respond to myriad climatic, environmental, temporal, social, and life-history factors (Caraco 1979, Jorde et al. 1984, Paulus 1988a, Davis and Smith 1998, Arzel et al. 2007). Wildlife managers can use activity budget data to determine the fundamental requirements of a species (Tamisier 1978-1979, Ashkenazie and Safriel 1979, Goldstein 1988), identify important wetland habitats and microhabitat characteristics (Frederickson and Drobney 1979, Jorde et al. 1984, Paulus 1984a, Paulus 1988b), and, ultimately, guide wetland management objectives designed for conserving or managing bird populations (Frederickson and Drobney 1979, Kaminski and Prince 1981, Quinlan and Baldassarre 1984, Paulus 1988b, Krapu et al. 1995, Sutherland 1998).

Among birds, one of the most intensively studied taxa are waterfowl (order Anseriformes) with over 100 studies having been published on the activity budgets of Anatids during the past forty years. Due to strong seasonal variation in climate and resource availability, most temperate- and subarctic-breeding waterfowl have regular and predictable annual cycles that are centered on spatially and temporally isolated life history events, such as pair-formation, migration, breeding, molting, and wintering (Johnsgard 1975, Johnsgard 1978, Bellrose 1980, Oring and Sayler 1992). These key life history events often involve a shift in resource requirements (e.g., nutritive or habitat), and consequently, a distinct seasonal redistribution of activity budgets. The activity budgets and diet choice of birds during winter and spring will affect body condition (i.e., fat and protein reserves), which influences the breeding success and survival of birds during the subsequent breeding season (i.e., cross-seasonal interactions; Ankney and MacInnes 1978, Krapu 1981, Myers 1981, Teunissen et al. 1985, Webster et al. 2002, Arzel et al. 2007, Devries et al. 2008). However, studies on the activity budgets of dabbling ducks (genus *Anas*) have focused on isolated phases of the annual cycle (e.g., breeding, wintering), and few studies have investigated the allocation of behavioral

activities in a single species over the entire annual cycle (Hickey and Titman 1983, Paulus 1984b, Arzel et al. 2007). Furthermore, even fewer studies have investigated the activity budgets and cross-seasonal interactions of tropical and isolated, island-endemic *Anas* species (Sorenson 1992, Reynolds 2002, Reynolds et al. 2010).

Non-migratory tropical and island-endemic dabbling ducks experience an entirely different suite of ecological demands than their migratory mainland counterparts (Terborgh and Winter 1980, Oring and Sayler 1992, Green 1996). Unlike the dramatic seasonal variation in climate experienced in temperate and subarctic regions, tropical regions may have mild climates and year-round resource availability. Lacking severe climatic and environmental pressures, many tropical dabbling ducks evolved sedentary life styles, either not moving among seasons or making relatively limited or short seasonal movements (e.g., from inland to coasts), while other tropical *Anas* make nomadic movements in response to rainfall and associated wetland availability (Frith 1959, 1982, Oring and Sayler 1992, Roshier et al. 2008). In isolated island systems, reduced mobility may conserve isolated island populations since migratory or nomadic behavior may reduce individual fitness (MacArthur and Wilson 1967, Weller 1980). Also, in tropical regions with stable climate and year-round resource availability, breeding at a particular time of year may not provide an overall advantage or disadvantage to survival and breeding success; therefore, individuals may vary considerably in the timing, duration, and synchronicity of the breeding season and molt cycle (Immelmann 1971, Siegfried 1974, Frith 1982, Sorenson 1992, Weller 1980, Oring and Sayler 1992, Young 2006). Accordingly, the daily and seasonal behavioral activity budgets of tropical *Anas* may vary significantly from North American migratory *Anas* (McKinney et al. 1978, McKinney 1992). Furthermore, many of the generalizations related to *Anas* behavior, habitat use, and fundamental resource requirements 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 (koloa maoli, *Anas wyvilliana*), closely related to the widespread Mallard (*A. platyrhynchos*), is one of two endemic species of *Anas* extant on the Hawaiian Islands (Olson and James 1982, Browne et al. 1993, Rhymer 2001).

Similar to many tropical dabbling ducks, the Hawaiian Duck evolved in response to relatively mild climatic and environmental conditions. As a result, the Hawaiian Duck has an extended breeding season and exhibits marked asynchrony in breeding schedules (Swedberg 1967). Although most of the limited nesting records on Kaua'i are between December and May, the Hawaiian Duck breeds year-round (Swedberg 1967, Engilis et al. 2002, USFWS 2011) and is non-migratory, presumably making only relatively short daily movements and some seasonal, intra- and inter-island movements (Perkins 1903, Swedberg 1967, Engilis et al. 2002, Malachowski and Dugger, unpubl. data). Once common on all of the main Hawaiian Islands except Lāna'i and Kaho'olawe (Perkins 1903, Olson and James 1982), the Hawaiian Duck experienced significant population declines during the twentieth century (Schwartz and Schwartz 1953, Banko 1987) and was extirpated from all islands within their historic range except Kaua'i and Ni'ihau by 1962 (Swedberg 1967). The primary reasons for species decline included wetland habitat loss and degradation, overexploitation, and introduced mammalian predators (Henshaw 1902, Swedberg 1967, Banko 1987). More recently, hybridization with feral Mallards has threatened remaining populations (e.g., O'ahu, Maui, Hawai'i) with loss of genetic integrity (Browne et al. 1993, Engilis et al. 2002, Uyehara et al. 2007, Fowler et al. 2009). Due to these pressures, the Hawaiian Duck was listed as Federally endangered in 1967 (USFWS 1967) and currently has the highest recovery priority among the four endangered waterbirds that occur on the main Hawaiian Islands (USFWS 2011).

One of the objectives for Hawaiian Duck recovery is to establish a protected and managed network of critical wetland habitat (USFWS 2011). Habitat restoration and management activities conducted by state and federal agencies began in the latter portion of the 20th century in the Hawaiian Islands and included the establishment of Hanalei, Hulē'ia, and James Campbell NWRs (USFWS 2011). While several studies have investigated wetland management techniques and agricultural practices on these NWRs (e.g., Chang 1990, Gee 2007, Wirwa 2007, Gutscher-Chutz 2011), none have quantified and compared Hawaiian Duck use of major habitat types and behavioral response to wetland habitat management. Whereas the response of North American migratory *Anas* to wetland management has been researched extensively, and habitat management

techniques have been refined over decades of work, the specific habitat needs and use of managed wetlands is virtually unknown for tropical dabbling ducks, such as the Hawaiian Duck, that may use the same wetland system throughout the annual cycle. Rather than providing resources to compliment one specific period of a species' annual cycle (e.g., winter), wetland management objectives in the Hawaiian Islands must provide habitat for Hawaiian Duck and other endangered waterbirds throughout the entire annual and life cycle of the species. However, a critical obstacle in developing effective habitat management plans for Hawaiian Duck involves the paucity of information on the patterns of habitat use in relation to fundamental daily resource requirements (e.g., foraging and roosting habitat) and seasonal life history requirements (e.g., breeding and molting habitat) of this species. By quantifying Hawaiian Duck behavioral patterns in natural wetlands and agricultural habitat (i.e., taro) within these protected areas, it is possible to assess the relative roles provided by habitat types and the period of the year when each is most important.

In this thesis I examined similarities and differences in the behavioral repertoire of the Hawaiian Duck and closely related island-endemic waterfowl and migratory North American *Anas,* I investigated how various factors (e.g., wetland habitat type) influenced the behavioral activities of the Hawaiian Duck, and I explored whether Hawaiian Ducks exhibited seasonal changes in key behaviors, such as courtship and foraging. The specific objectives of this study were to: 1) describe the behavioral repertoire of male and female Hawaiian Ducks, 2) quantify and compare the behavioral response of the Hawaiian Duck to wetland habitat management and taro cultivation, and 3) investigate the effects of environmental, climatic, temporal, and social factors on the activity budget of Hawaiian Ducks. I predicted that the behavioral repertoire of the Hawaiian Duck would be very similar to that of the Mallard due to their close genetic relationship and the lack of strong climatic and ecological pressures that would drive the evolution of a unique set of behaviors. However, I expected that Hawaiian Ducks would allocate less time to foraging than North American *Anas* species due to their non-migratory nature and potentially lower daily and seasonal energy demands. I also predicted that Hawaiian Ducks would exhibit only subtle seasonal variation in overall time-activity budgets due to

their apparent asynchronous annual cycle and sedentary lifestyle. If any seasonality in life-history events occurred, I expected it to be most evident in the proportion of time allocated to courtship behaviors during pair-formation. Last, I predicted that Hawaiian Ducks would utilize managed and agricultural wetlands for different activities (e.g., greater foraging activity in managed wetlands) due to differences in wetland characteristics (e.g., vegetation cover and structure) and resource availability.

STUDY AREA

My study was conducted at Hanalei National Wildlife Refuge (NWR) on the north shore of Kauaʻi County, Hawaiʻi (21° 12.052' N, 159° 28.352' W; Fig. 1). Situated in the lower Hanalei River Valley, this 371 ha refuge has 24.4 ha of managed wetland habitat (KNWRC 2008) and 53.0 ha of cultivated taro (kalo, *Colocasia esculenta*) loʻi (Gee 2007). Taro is a traditional Hawaiian food source and farmed in shallowly flooded fields, or loʻi, similar to rice paddies. Ditches and dikes account for 25.8 ha of refuge area (KNWR 2008, Gee 2007). The remainder of Hanalei NWR consists of ephemerally flooded pasture (36 ha), lowland forest (224 ha), and riverine habitat (Asquith and Melgar 1998, KNWR 2008).

The Hanalei River headwaters form on Mount Waiʻaleʻale (1,569 m elevation) and flow 25.2 km north to Hanalei Bay. The lower 5.6 km section of the Hanalei River flows through Hanalei NWR where water is diverted to taro loʻi and managed wetlands. Precipitation at Hanalei NWR varies between a relatively dry season (10.9 – 16.4 cm/mo from May to October) and a wet season (17.3 – 23.1 cm/mo from November to April); mean annual rainfall at Hanalei NWR is 208.8 cm/yr (NCDC 2012; Appendix A). In addition, precipitation on Kauaʻi varies significantly with altitude and latitude, and between Hanalei NWR and Mount Waiʻaleʻale (1,010 cm/yr), precipitation increases by over 50 cm/km (NCDC 2012). Temperatures at Hanalei NWR fluctuate very little throughout the year. The mean high temperature is 25.3° C in February and 29.4° C in August; the mean low February and August temperatures are 17.2° and 20.7° C, respectively (NCDC 2012; Appendix B)

Hanalei NWR was established in 1972 under the Endangered Species Act to aid in the recovery of endangered Hawaiian waterbirds through the preservation and management of critical habitat. The refuge supports five endangered birds including the Hawaiian Duck, Hawaiian Coot (*Fulica alai*), Hawaiian Common Moorhen (*Gallinula chloropus sandvicensis*), Hawaiian Black-necked Stilt (*Himantopus mexicanus knudseni*), and Hawaiian Goose (*Branta sandvicensis*). The islands of Kauaʻi and Niʻihau may support approximately 90% of remaining non-hybridized Hawaiian Ducks (Engilis and Pratt 1993, Engilis et al. 2002), and Hanalei is believed to be the single most important low elevation wetland site on those islands (Banko 1987, USFWS 2011).
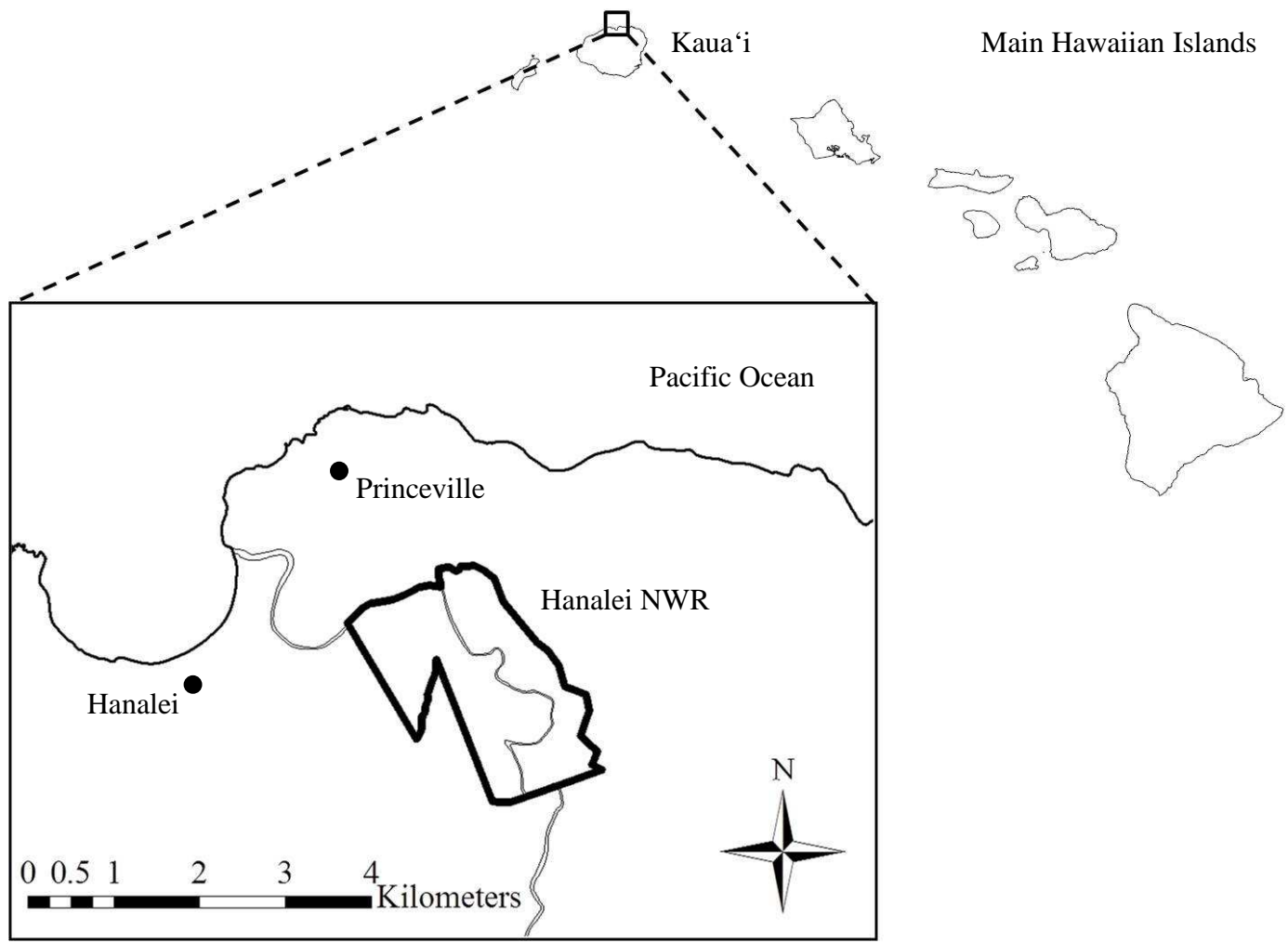
Figure 1. Map of the main Hawaiian Islands with detail of Hanalei National Wildlife Refuge, Kaua'i.

METHODS

BEHAVIORAL OBSERVATIONS

I selected a representative sample of managed wetlands ($n = 6$) and taro complexes ($n = 6$) from those in Hanalei NWR as focal areas for collecting data on Hawaiian Duck behavior (Fig. 2). Complete randomization of study sites was not feasible due to refuge regulations and potential disturbance to endangered waterbirds. Of the 13 actively managed wetland impoundments at Hanalei NWR, I selected six units based on the criteria of maximizing visibility of wetland, minimizing disturbance to endangered waterbirds, and including a representative sample of units in various management stages. The area of managed wetland study units ranged from 0.83 ha to 3.26 ha (Appendix C). Of the 290 taro loʻi on the refuge, I selected 33 loʻi that were grouped into six complexes of four to eight loʻi each. The size of individual loʻi ranged from 0.09 to 0.49 ha, and the area of loʻi complexes ranged from 0.85 to 1.55 ha (Appendix C). These six complexes were distributed across the refuge and included a variety of taro stages. Additionally, I selected units that represented a diversity of taro farming styles; sampling sites were farmed by five of the nine taro leaseholders on the refuge.

Surveys were conducted from 3.0 m high tower blinds or from blinds located on hillsides. I randomized the order that sites were visited on a weekly basis. For each month, I stratified behavior surveys by time of day, which was divided into four periods: 30 min before sunrise to late morning (early morning), late morning to midday (late morning), midday to early evening (afternoon), and early evening to 30 min after sunset (evening). To calculate duration of each period, I divided the duration of daylight (i.e., 30 min before sunrise to 30 min after sunset) into the four sampling periods.

After arriving at survey sites, I scanned the survey area for 5-10 min and counted the number of male and female Hawaiian Ducks in each habitat type. Habitat types were broadly classified as managed wetland and taro. Within each habitat type, I recorded if individuals were in the unit or on a dike. Within taro, I categorized cover classes as taro, wet or dry non-vegetated fallow, wet or dry fallow with predominantly non-taro emergent vegetation, and harvested. To minimize the chance of recording observer-influenced behavior, I waited at least 5 min after arriving at survey sites before beginning behavior

surveys; however, in most (86.0%, 846 of 984) surveys this wait time was ≥ 10 min (mean = 31.6 min, median = 21.8 min). I randomly selected focal individuals for behavioral sampling by counting the total number of Hawaiian Ducks (i) at the survey site, obtaining a random number (j) from column i of a random number chart, and counting birds left to right until I reached the jth individual. Focal observations were not conducted on ducklings; however, females with broods were sampled. I assumed birds selected for focal observation were different individuals. It is possible that the same birds were sampled on more than one occasion; however, given the relatively large number of birds observed at Hanalei NWR (e.g., 323 ± 23, based on diurnal surveys conducted between March and August 2011, $n = 6$; Malachowski and Dugger, unpubl. data) and our use of randomization procedures, this was unlikely to significantly affect results.

I used instantaneous focal sampling procedures (Altmann 1974) to quantify the time-activity budgets of Hawaiian Duck between September 2010 and August 2011. I recorded the behavioral activity of focal individuals at 10 sec sample intervals using a digital voice-activated recorder and electronic timer (Baldassarre et al. 1988, Dugger and Petrie 2000). I observed birds with a 20-60x spotting scope or 10x binoculars from approximately 7-315 m away. Since the complete behavioral repertoire including specific foraging, courtship, display, and social behaviors has not been fully described for the Hawaiian Duck (Engilis et al. 2002), I inventoried the behavioral activities of Hawaiian Duck prior to the main study period. Additional behaviors and descriptions were added to the inventory as they occurred during the field season (Appendix D). Due to the similar behavioral repertoire between the Hawaiian Duck and Mallard, I adopted behavior terminology derived for Mallard (Lorenz 1951, Johnsgard 1960, Johnsgard 1965, McKinney 1965). I classified Hawaiian Duck behavioral repertoire into 73 distinct behavioral activities; however, for most analyses, I grouped behaviors into six general behavioral categories: foraging, resting, maintenance, locomotion, alert, and social (includes courtship, intraspecific agonistic interactions, and interspecific agonistic interactions). Instantaneous behaviors were recorded as events and states, where events were instantaneous occurrences of a behavior, and states occurred in a continuum (Altmann 1974). For example, a bird that briefly paused between dabbling bouts was in a

foraging state. Behavioral states and events were combined to determine the total proportion of time for each behavior. Since many courtship behaviors involved modified maintenance movements, I differentiated between these two states based on the orientation and proximity of focal individuals to females and males, the nature of interactions among conspecifics, and the overall context of the situation (McKinney 1965). In situations where the function of these movements was not apparent, behaviors were classified under maintenance activities; however, most courtship behaviors were clearly evident. All data were collected by one observer.

When focal birds moved out of sight, I recorded behavior as "out of view" until the individual returned into view. No "out of view" observations were included in analyses or used to calculate total survey time. If the focal individual remained out of view, left the survey site, or switched habitat types, and if a bird of similar sex, age, and pair status was present in the same habitat type and cover class at the survey site, I continued the observation session by watching the alternate bird (Losito et al. 1989); otherwise, the session would end. To maximize the independence of behavioral responses among focal samples, no more than one behavioral observation session was conducted per survey site per time period in a given day, and most (94.0%, 925 of 984) observation sessions at a given survey site were separated by ≥ 1 day. Observation sessions lasting between 5-30 min (mean = 20.0 min, median = 20.0 min) were used for subsequent analyses because I did not want to bias samples towards more sedentary behaviors that may occur more frequently in longer sessions or more active behaviors that may occur during shorter sessions. Furthermore, the differences in variance between samples of varying duration were inconsistent, sample sizes were large, and sample durations were relatively evenly distributed among months, time of day, and habitat types.

During observation periods, I determined the sex and age (juvenile or adult) of each focal individual using plumage characteristics (Engilis et al., unpubl. data). Since birds in formative and first alternate plumage (i.e., first year birds) were not always discernible from birds in definitive basic and alternate plumage, they were grouped with adults. Pair status of focal individuals was recorded at the end of each observation

session. To avoid mistaking temporary associations with paired status, I classified birds as paired only if they 1) exhibited synchronized activities (particularly, agonistic behaviors), 2) maintained a close spatial relationship (approximately 3.0 m) during most of the observation session, and 3) mutually avoided or threatened other Hawaiian Ducks when nearby (Paulus 1983). I also recorded if focal individuals associated with possible Mallard-Hawaiian Duck hybrids on a sample interval. Hybrids were identified based on plumage characteristics (Engilis et al., unpubl. data).

Instantaneous climate variables were recorded at 5 min intervals and then averaged over the focal observation period. I measured wind velocity (km/hr) using a handheld anemometer, and I estimated cloud cover (%) and precipitation intensity (0 = none, 1 = light, 2 = moderate, and 3 = heavy). Monthly climate variables (total rainfall and mean temperature) were obtained from a USGS climate station at Princeville Ranch, approximately one km north of Hanalei NWR (NCDC 2012). In addition, anthropogenic disturbances to focal individuals were recorded.

To test the hypothesis that birds allocate activity budgets differently during various life history events, I defined two seasons – brood rearing (December-May) and pair formation (November-March). While Hawaiian Duck may breed throughout the year on Kaua‘i, Swedberg (1967) observed 72% of broods between December and May ($n = 64$). Similarly, the extrapolated hatch date of 61% of unique broods detected on Kaua‘i during my study period was between December and May ($n = 72$; Appendix E). Pair formation may also occur throughout the year; however, most observations suggest a peak in pair formation between November and March (Swedberg 1967, Engilis et al. 2002).

MANAGED WETLAND SAMPLING

I used quadrat sampling procedures to characterize habitat features within each of the six managed wetland units selected for behavioral sampling at Hanalei NWR. Thirty sampling points were randomly selected for each managed wetland. For the three small, adjacent rice mill units, I randomly selected ten sample points per unit. To select sampling points within each site, I recorded the perimeter of the sampling site using a

handheld Global Positioning System (GPS) unit, imported the location data into a Geographical Information System (GIS; ESRI ArcGIS version 9.3, 2008), and used the "Create Random Points" tool in the "Data Management Tools" toolbox." I uploaded the resultant sampling points into a GPS unit that I used to locate each point (accuracy ≤ 4.0 m). I marked sampling points with a pin flag. I then used a random number generator to select the angle at which each 1.0 x 0.5 m quadrat was positioned on the sampling point.

At each sampling point I measured water depth and emergent vegetation height at the pin flag. Within each quadrat, I visually estimated total vegetation cover, vegetation cover by species, and percentage of sub-canopy open water, and I measured maximum vegetation height. I sampled wetlands in September 2010 and every other month between October 2010 and August 2011. During each sampling session, I returned to the same sampling point locations and used the same randomly selected bearings to orient the quadrat. If I could not relocate pin flags (4.0% of samples), I used a GPS unit to relocate and remark the sampling point (accuracy ≤ 4 m). I summarized monthly sampling data within each wetland sampling site by calculating the means of each wetland habitat variable.

STATISTICAL ANALYSES

Activity data were converted to proportions of time engaged in each behavior during each focal observation session (Baldassarre et al. 1988). Logit transformations were applied to proportions before analyses to improve homogeneity of variances and meet the assumption of normality (Ramsey and Schafer 2002). I used individual focal observation sessions as the sample unit to determine the relationship between dependent variables (proportion of time engaged in each behavioral state) and explanatory variables (e.g., habitat type, time of day, sex, pair status, and month). Since 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), factorial multivariate analysis of variance (MANOVA) using Wilks' lambda test criterion was used to simultaneously evaluate the effects of explanatory variables on time-activity budgets (Ramsey and Schafer 2002).

If MANOVA indicated significant effects of explanatory variables ($P < 0.05$), univariate analysis of variance (ANOVA) was used to further examine the effects on separate behaviors after controlling for all other explanatory variables. To assess the effect of pair status on activity budgets, focal samples conducted on birds with undetermined pair status, juvenile birds, and females with broods were removed from analysis. If logit transformations failed to normalize the data and satisfy the equal variance assumption, I used the Kruskal-Wallis test to compare the untransformed proportion of time engaged in the activity between explanatory variables (Ramsey and Schafer 2002). The Kruskal-Wallis test was also used to evaluate the effects of explanatory variables on specific foraging and social behaviors (i.e., courtship and display, intra-specific agonistic activities, and inter-specific agonistic activities).

I used Spearman correlation analysis to examine the relationship between behavioral activities and managed wetland habitat variables and climate variables. I used Fisher's exact test (Ramsey and Schafer 2002) to assess if the proportion of focal samples involving anthropogenic disturbances differed between managed wetland and taro regions. To determine the relative frequency of occurrence of each behavior within a behavior category, I divided the mean proportion of time engaged in the behavior (e.g., dabbling) by the mean proportion of time engaged in the behavior category (e.g., foraging).

For parametric and non-parametric procedures, I 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). All time-activity budget values are reported as untransformed means ± standard error (SE).
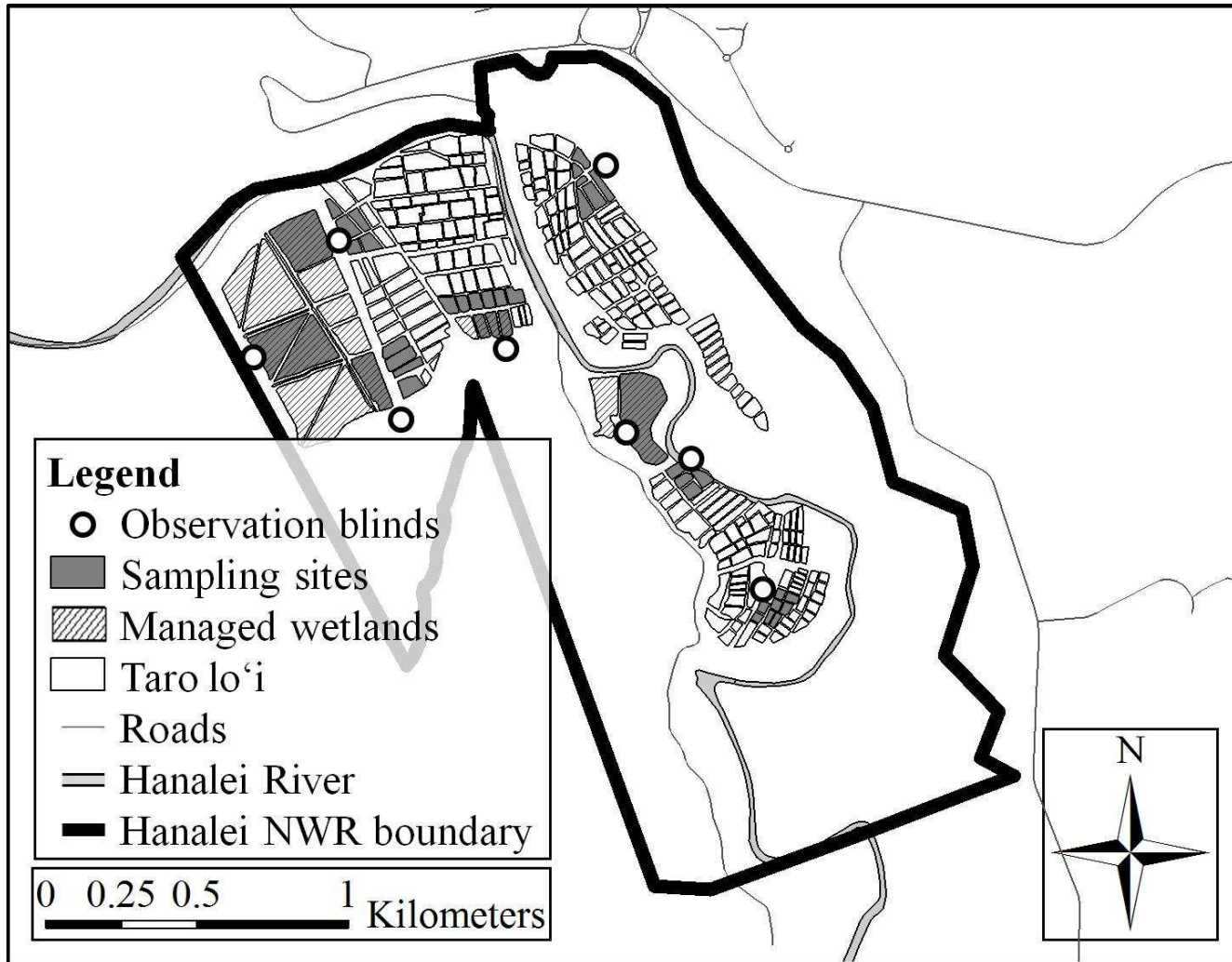
Figure 2. Distribution of managed wetlands and taro loʻi, including sampling sites, at Hanalei National Wildlife Refuge, Kauaʻi.

RESULTS

Between September 2010 and August 2011, I collected 1,364 focal samples on Hawaiian

Duck totaling 369.4 hours. From this dataset, 984 focal samples from 224 females and

760 males totaling 328.8 hours met the criteria for these data analyses (Table 1). The

population of Hawaiian Duck at Hanalei NWR was biased towards males, and the

proportion of females in the population ranged from 36% in September 2010 to 22% in

February 2011 (monthly mean = $29.0 \pm 1.2\%$, $n = 3089$ birds). The mean percentage of

paired females was highest between November and March (i.e., peak pair-formation

months), when $80.3 \pm 6.5\%$ of focal adult females were paired (Fig. 3). The percentage

of paired, adult females dropped to $59.3 \pm 6.9\%$ during the remainder of the year. The

proportion of paired, adult males peaked in September (66.7%) and October (72.7%) and

declined to $15.7 \pm 1.8\%$ during the remainder of the year.

Hawaiian Ducks were most frequently observed singly or in pairs; however, small

groups of three to ten birds, particularly bachelor males, were common throughout the

year. While uncommon, larger concentrations (> 10 individuals per complex) were more

frequently observed between June and September than other months. The largest flock of

Hawaiian Ducks observed in any single managed wetland unit was 124 birds (in unit

DU2) during July 2011. Although not occurring during a count survey, the largest flock

of Hawaiian Ducks observed during the field season was 271 ducks (also in DU2 in July),

and the largest flock counted in a taro lo'i was 110 birds in a single non-vegetated wet

fallow in May 2011. These larger concentrations of Hawaiian Ducks were observed

during evenings.

Focal Hawaiian Ducks were observed near possible Mallard-Hawaiian Duck

hybrids in 1.9% ($n = 19$) of observation sessions. Possible male hybrids associated with

Hawaiian Ducks, joined courting groups, and displayed to Hawaiian Duck females.

Differences in display behaviors between hybrids and Hawaiian Ducks were not

qualitatively noticeable. Female Hawaiian Ducks were paired with possible hybrid

Mallard-Hawaiian Ducks in 1.3% ($n = 3$) of observation sessions in which the female was

the focal individual.

HAWAIIAN DUCK BEHAVIORAL REPERTOIRE

I documented 73 specific Hawaiian Duck behaviors in eight broad behavior categories including foraging, maintenance, resting, locomotion, alert, courtship, and intra- and interspecific agonistic interactions (Appendix D).

Foraging behaviors

Hawaiian Ducks were observed using ten foraging behaviors. Head-dipping, dabbling, and probing were the most common foraging tactics and constituted 51.0%, 30.9%, and 8.1% of time spent foraging pooled among all habitat types (Table 2). Birds were observed dabbling seeds (e.g., *Ludwigia octovalvis*, *Cyperus* spp.), filamentous green algae (Chlorophyceae), duckweed (*Lemna aequinoctialis*), and large mosquito fern (*Azolla filiculoides*) from the water surface. Nibbling the seeds, leaves, and inflorescences of vegetation accounted for 2.7% of foraging time and included *L.octovalvis*, *Cyperus* spp., *Fimbristylis littoralis*, *Fimbristylis dichotoma*, *Schoenoplectus juncoides, Echinochloa crus-galli, Paspalum* spp., and others. A relatively common form of this foraging behavior involved stripping or breaking the seed pods of *L. octovalvis* and dabbling the released seeds off the surface of the water column. Hawaiian Ducks also accessed the seed heads of taller *Cyperus* spp. by walking or swimming over the base of the plant, bending the seed head into the water, and then nibbling and dabbling the seeds from the water surface. Birds probed in mud and matted vegetation, particulary *F. littoralis*, to access seeds and invertebrates, such as snails (Gastropoda) and worms (Oligochaeta). Diving was observed infrequently and never occurred during a focal observation session.

Maintenance, resting, locomotion, and alert behaviors

I recorded 16 maintenance behaviors of the Hawaiian Duck, but preening was most common, accounting for 90.1% of maintenance time (Appendix F). Locomotor behaviors involved swimming, walking/running, and flying (not associated with courtship or agonistic interactions), which comprised 76.8%, 18.5%, and 4.7% of locomotion time, respectively (Appendix F). Time spent flying was considered an

underestimation, because flying behavior was not recorded once birds exited the observation area. Resting behaviors included loafing and sleeping with head tucked back or bill drawn in close to chest. Resting behaviors were not differentiated, except for brooding which accounted for 0.4% of resting behavior. Alert behavior among Hawaiian Ducks typically involved maintaining an upright, erect posture and extending the neck while motionless or scanning (94.2%). Vocalizing, head-pumping, sky-looking, flushing, and bill-flicking each accounted for less than 2.5% of time spent in alert behavior. Birds infrequently escaped disturbances by swimming just below the water surface (i.e., submerged swimming), but this behavior did not occur on a focal sample interval.

Courtship behaviors and pair formation

I documented 20 distinct courtship behaviors (Appendix D). Courtship displays among male Hawaiian Ducks most frequently involved various shakes, including head-shaking, tail-wagging, body-shaking, and wing-flapping, which accounted for 24.6%, 14.7%, 6.5%, and 4.5% of courtship observations, respectively. Grunt-whistles, head-up-tail-up, and down-up displays combined for 22.2% of male courtship behavior, while nod-swimming accounted for 10.1%. Head-up-tail-up displays were frequently followed by nod-swimming; however, the nod-swimming display occasionally followed the grunt-whistle and down-up displays or occurred independent of any precursor display. Dash-and-dive and jump-flight displays were usually, though not exclusively, performed by males. Primary display behaviors of females included inciting and nod-swimming. Both sexes partook in nuptial flights, which accounted for 7.3% and 22.9% of male and female courtship behavior, respectively; however, this is considered an underestimation since this behavior was not recorded after birds flew out of view or exited the study area.

I witnessed 20 copulation events, and seven of these events occurred during focal sampling. Copulation usually occurred in water ($n = 18$); however, two forced copulation events occurred on dikes or matted vegetation. Typically, copulation was immediately preceded by shallow pre-copulatory head-pumping from the male as the female performed nod-swimming and/or assumed the pre-copulatory prone position (i.e., partially submerged with flattened body and neck extended). Post-copulatory behavior

often involved vigorous preening and bathing, nod-swimming, wing-flapping, various shakes, bridling, dash-and-dive displays, turning-the back-of-the-head, and/or leading.

Agonistic interactions

Intraspecific agonistic behaviors among Hawaiian Duck involved threats and aggression (44.7%), receiving aggression and submission (29.9%), and mate-guarding (25.4%). Threats and aggressive behavior included bill-flicking, bill-jabbing, bill-pointing, bill-threatening, chasing, feather-pulling, forced copulation, inciting, pecking, pursuit flights, vocalizing, and wing-flapping. Paired females incited mates to attack selected individuals; however, unpaired and paired females also performed inciting displays, presumably to express agitation towards nearby males. Paired males vigilantly and persistently guarded mates by maintaining an alert posture and positioning themselves between their mate and other males. Paired males also mate-guarded by escorting other males away from females. These guarding behaviors often escalated into more aggressive threats and chases. Gestures of repulsion were occasionally performed by harassed or brood-tending females towards intruding males, and males occasionally attempted forced copulation with females; however, those behaviors were not detected on a focal sample interval. Hawaiian Ducks also engaged in agonistic behavior with possible Mallard-Hawaiian Duck hybrids in eight observation sessions.

Interactions between Hawaiian Duck and Hawaiian Common Moorhen, Hawaiian Coot, Hawaiian Black-necked Stilt, and Hawaiian Goose accounted for 49.5%, 25.2%, 14.0%, and 7.0% of interspecific agonistic activity, respectively (Appendix G). Agonistic interactions occurred less frequently with Common Myna (*Acridotheres tristis*), Cattle Egret (*Bubulcus ibis*), migratory Lesser Scaup (*Aythya affinis*), Pacific Golden Plover (*Pluvialis fulva*), and Nutmeg Mannakin (*Lonchura punctulata*). Overall, 90.1% of interspecific interactions involved aggression towards or submission by Hawaiian Ducks. While migratory Anatids (Appendix H), including several species of Anatini (e.g., Northern Pintail [*Anas acuta*], Northern Shoveler [*Anas clypeata*], American Wigeon [*Anas americana*], Green-winged Teal [*Anas crecca*], Mallard), occurred at Hanalei NWR during the sampling period, flocks and individuals generally

remained separated from Hawaiian Duck and interactions were rare (< 1% of interspecific agonistic activity).

TIME-ACTIVITY BUDGETS

Effects of habitat type and wetland characteristics

After accounting for sex, pair status, month, and time of day, behavioral activities of Hawaiian Ducks differed between managed wetlands and taro habitats (MANOVA; Wilks' $\lambda = 0.84$, $F_{6,960} = 30.3$, $P < 0.001$). The effect of habitat type was significant for all behavioral categories except alert behavior (Table 3). In managed wetlands, the activity budgets of Hawaiian Ducks were relatively evenly distributed between maintenance, resting, locomotion, and foraging. Conversely, birds used taro predominantly for resting (44.3%), maintenance (21.3%), and foraging (15.0%). Within taro the behavioral activities of Hawaiian Ducks differed significantly between birds in lo'i and on dikes (MANOVA; Wilks' $\lambda = 0.35$, $F_{6,468} = 142.8$, $P < 0.001$; Appendix I). Hawaiian Ducks utilized taro lo'i dikes for resting (60.0%) and maintenance activities (21.1%), whereas birds entered lo'i primarily to forage (44.8%).

Hawaiian Ducks spent a slightly greater proportion of time foraging when using taro than when using managed wetlands. Among taro cover classes (excluding samples on dikes), birds spent the greatest percentage of time foraging in harvested lo'i (62.8%) and the least in non-vegetated dry fallow (22.6%; Appendix J). In managed wetlands, foraging behavior was negatively correlated with mean emergent vegetation height and mean water depth (Table 4). Hawaiian Ducks foraged slightly more with increasing cover of *Cyperus* spp. and *F. littoralis* and with decreasing cover of *U. mutica* and *L. octovalvis*. The primary foraging tactics used by Hawaiian Duck were head-dipping and dabbling; however, birds allocated foraging tactics differently between managed wetlands and taro (MANOVA; Wilks' $\lambda = 0.97$, $F_{10,956} = 3.15$, $P < 0.001$; Table 2). Probing in mud and matted vegetation constituted a larger proportion of foraging behavior within managed wetlands (13.9%) than taro (3.8%), whereas birds spent more foraging time head-dipping in taro (56.1%) than in managed wetlands (44.1%).

Hawaiian Ducks allocated more time to resting when using taro (44.3%) compared to managed wetlands (26.8%), and within taro, birds rested significantly more on dikes (60.0 ± 1.6%) than in lo'i (12.7 ± 1.9%; ANOVA, $F_{1,473} = 361.7$, $P < 0.001$). In managed wetlands, birds allotted more time to maintenance (28.3% vs. 21.3%) and locomotion (22.0% vs. 7.5%) than in taro. Human-related disturbance was similar among managed wetlands (10.4%) and taro (14.0%; Fisher's exact test, $P = 0.097$; Appendix K).

The proportion of time engaged in social behaviors by birds was generally low, but higher in managed wetlands (1.3%) than in taro (0.5%). More specifically, courtship occurred significantly more frequently in managed wetlands (0.5 ± 0.1%) than in taro (< 0.1%; Kruskal-Wallis, $H_1 = 26.8$, $P < 0.001$), and copulation, which occurred in 1.4% of observation sessions in managed wetlands, did not occur in any samples in taro.

Daily and seasonal variation in behavior

Time activity budgets varied significantly across time of day (MANOVA; Wilks' $\lambda = 0.89$, $F_{18,2715.78} = 6.4$, $P < 0.001$). The effect of time of day was significant for foraging (Kruskal-Wallis, $H_3 = 34.8$, $P < 0.001$), resting (ANOVA, $F_{3,965} = 16.3$, $P < 0.001$), alert (ANOVA, $F_{3,965} = 9.8$, $P < 0.001$), locomotion (ANOVA, $F_{3,965} = 8.8$, $P < 0.001$), and maintenance (ANOVA, $F_{3,965} = 5.9$, $P < 0.001$) behaviors, but not for social behaviors (Kruskal-Wallis, $H_3 = 7.53$, $P = 0.057$). Across all habitat types, birds allotted more time to active behaviors, such as foraging, locomotion, and alert behavior, and less time to resting during early morning and evening than during late morning and afternoon (Table 5).

The activity budgets of Hawaiian Duck also varied monthly (MANOVA, Wilk's $\lambda = 0.89$, $F_{66,5142.3} = 1.70$, $P < 0.001$; Appendix M). Overall, the proportion of time engaged in alert behavior (ANOVA, $F_{11,965} = 3.57$, $P < 0.001$) and interspecific interactions (Kruskal-Wallis, $H_{11} = 26.8$, $P = 0.005$) differed significantly by month. Agonistic interactions between Hawaiian Duck and Hawaiian Black-necked Stilt occurred most frequently between April and July (Kruskal-Wallis, $H_1 = 10.0$, $P = 0.002$), while interactions with Hawaiian Common Moorhen (Kruskal-Wallis, $H_{11} = 18.85$, $P = 0.06$) and Hawaiian Coot (Kruskal-Wallis, $H_{11} = 18.40$, $P = 0.07$) varied only marginally

by month (Appendix N). The effects of rainfall intensity, cloud cover, wind speed, and monthly rainfall on the proportion of time birds spent in foraging, resting, social and alert behaviors were not significant.

On a seasonal basis, Hawaiian Duck slightly reallocated behavioral activities during months associated with peak pair formation (i.e., November through March; (MANOVA, Wilk's $\lambda = 0.97$, $F_{6,970} = 4.73$, $P < 0.001$). The mean proportion of time that males spent courting ($1.1 \pm 0.3\%$ vs. $0.3 \pm 0.1\%$; Kruskal-Wallis, $H_1 = 6.92$, $P = 0.009$; Fig. 4) and mate-guarding ($0.5 \pm 0.4\%$ vs. $< 0.1\%$; Kruskal-Wallis, $H_1 = 9.83$, $P = 0.002$) in managed wetlands was significantly higher between November and March than other months. Birds also engaged in slightly more alert behavior ($12.7 \pm 0.7\%$ vs. $9.9 \pm 0.5\%$,; ANOVA, $F_{1,975} = 29.17$, $P < 0.001$) and less foraging ($11.6 \pm 1.3\%$ vs. $14.0 \pm 1.1\%$; Kruskal-Wallis, $H_1 = 4.27$, $P = 0.039$) during peak pair formation months; however, the differences were subtle. The activity budgets of Hawaiian Ducks varied only marginally with peak brood rearing season (i.e., December through May; MANOVA, Wilk's $\lambda = 0.99$, $F_{6,970} = 1.79$, $P = 0.098$). Among females, brooding only occurred in 1.3% (3 of 224) of observation sessions, all of which occurred between November and March. While the proportion of time allocated to foraging did not depend on seasonal periods related to brood rearing, birds exhibited seasonal shifts in relative use of various foraging tactics. For example, probing constituted 22.4% of foraging activity during July and August, and only 3.8% of foraging activity during the remainder of the year.

Effects of sex and pair status

The behavioral activities of Hawaiian Duck differed slightly between sexes (MANOVA, Wilks' $\lambda = 0.96$, $F_{6,960} = 6.06$, $P < 0.001$; Table 6). The proportion of time spent foraging was significantly higher in females (17.5%) than in males (11.8%), and these sex-specific differences in foraging time were most evident between October and April (Kruskal-Wallis, $H_1 = 13.08$, $P < 0.001$) when females and males allocated $19.2 \pm 2.9\%$ and $9.4 \pm 1.0\%$ of time to foraging, respectively (Fig. 5). During the remainder of the year, females and males spent similar proportions of time foraging ($15.8 \pm 2.7\%$ vs. $14.8 \pm 1.5\%$, respectively; Kruskal-Wallis, $H_1 = 0.27$, $P = 0.604$). However, while

percentage of time spent foraging differed among months for males (Kruskal-Wallis, H_{11} = 21.2, P = 0.031), it did not differ for females (Kruskal-Wallis, H_{11} = 5.2, P = 0.921).

Overall, males spent a greater proportion of time engaged in alert and locomotor activities than females. Furthermore, males allocated more time to social activities, particularly courtship (Kruskal-Wallis, H_1 = 4.89, P = 0.027) and intraspecific agonistic interactions (Kruskal-Wallis, H_1 = 6.97, P = 0.008). The relative frequency of foraging behaviors used by male and female Hawaiian Ducks was similar (MANOVA, Wilks' λ = 0.99, $F_{10,956}$ = 1.07, P = 0.382).

Pair status also affected the behavioral patterns of Hawaiian Ducks (MANOVA, Wilks' λ = 0.94, $F_{6,682}$ = 6.69, P < 0.001), but the nature of those differences depended on habitat (MANOVA, Wilks' λ = 0.97, $F_{6,982}$ = 3.68, P = 0.001; Table 7). When using taro, paired birds foraged more (27.1% vs. 13.0%) and rested less (35.3% vs. 47.4%) than unpaired birds; time spent in these behaviors were similar for paired and unpaired birds using managed wetlands. Overall, paired birds were engaged in more social behavior (1.8%) than unpaired birds (0.7%), allocating more time to aggressive behavior towards conspecifics (Kruskal-Wallis, H_1 = 18.63, P < 0.001), mate-guarding (Kruskal-Wallis, H_1 = 25.50, P < 0.001), and courtship (Kruskal-Wallis, H_1 = 5.89, P = 0.020).
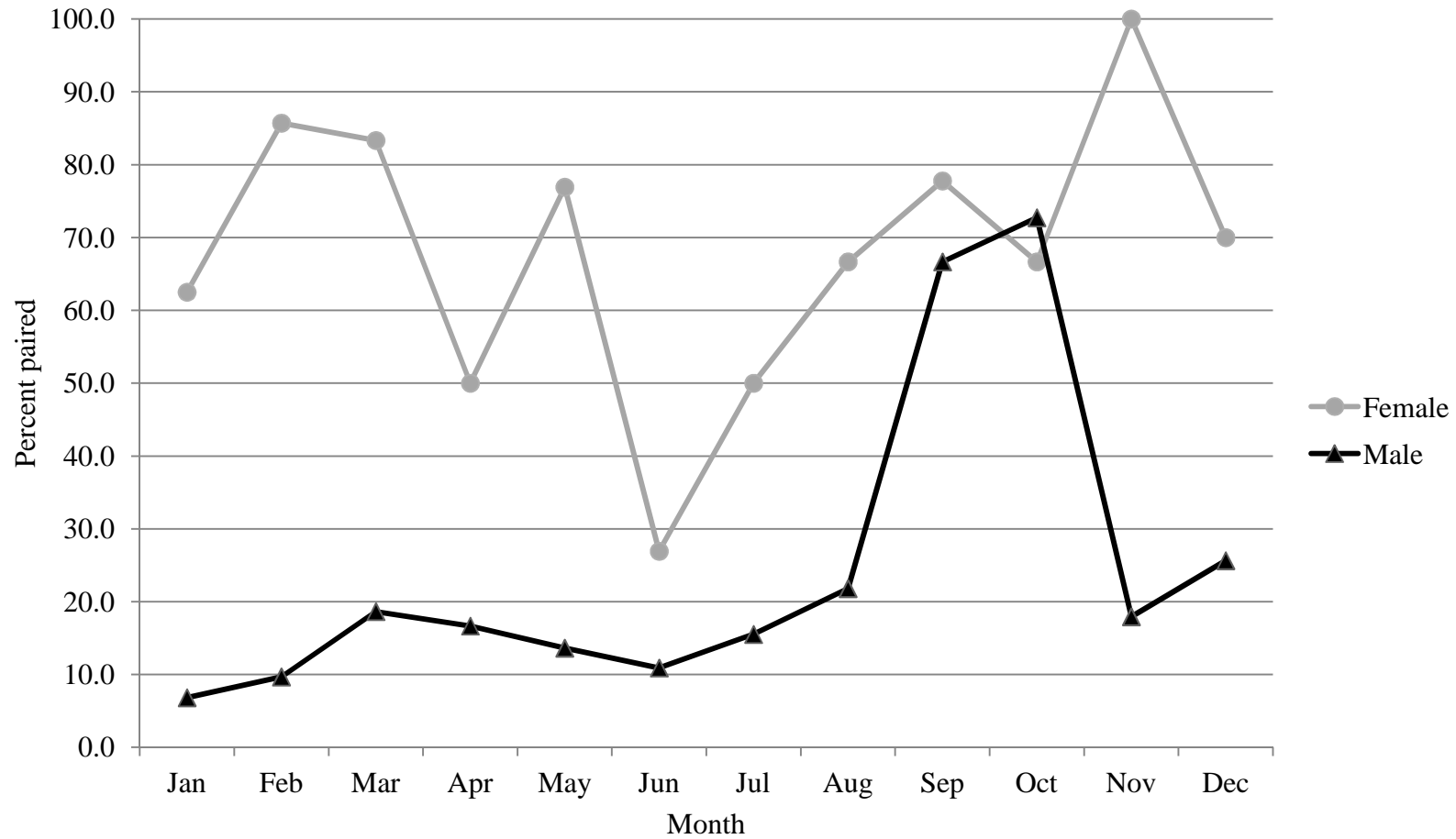
Figure 3. Monthly variation in the percentage of paired male and female Hawaiian Ducks (n_{male} = 557; n_{female} = 149) between September 2010 and August 2011 at Hanalei National Wildlife Refuge, Kaua'i.
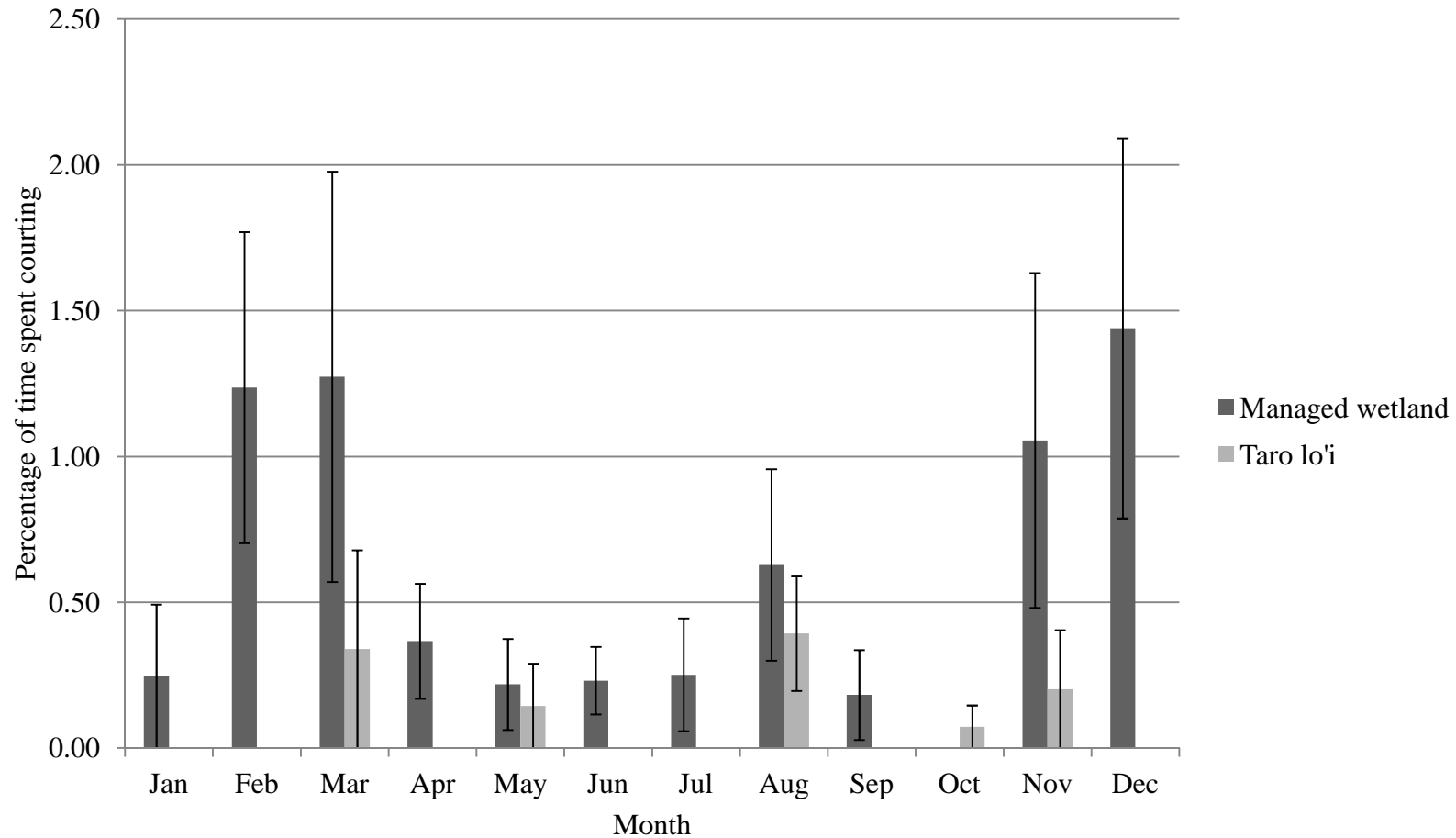
Figure 4. Monthly variation in the percent time ($\bar{x} \pm$ SE) male Hawaiian Ducks allocated to courtship activities in managed wetlands ($n = 388$ observation sessions) and taro loʻi ($n = 372$) at Hanalei National Wildlife Refuge, Kauaʻi from September 2010 to August 2011.
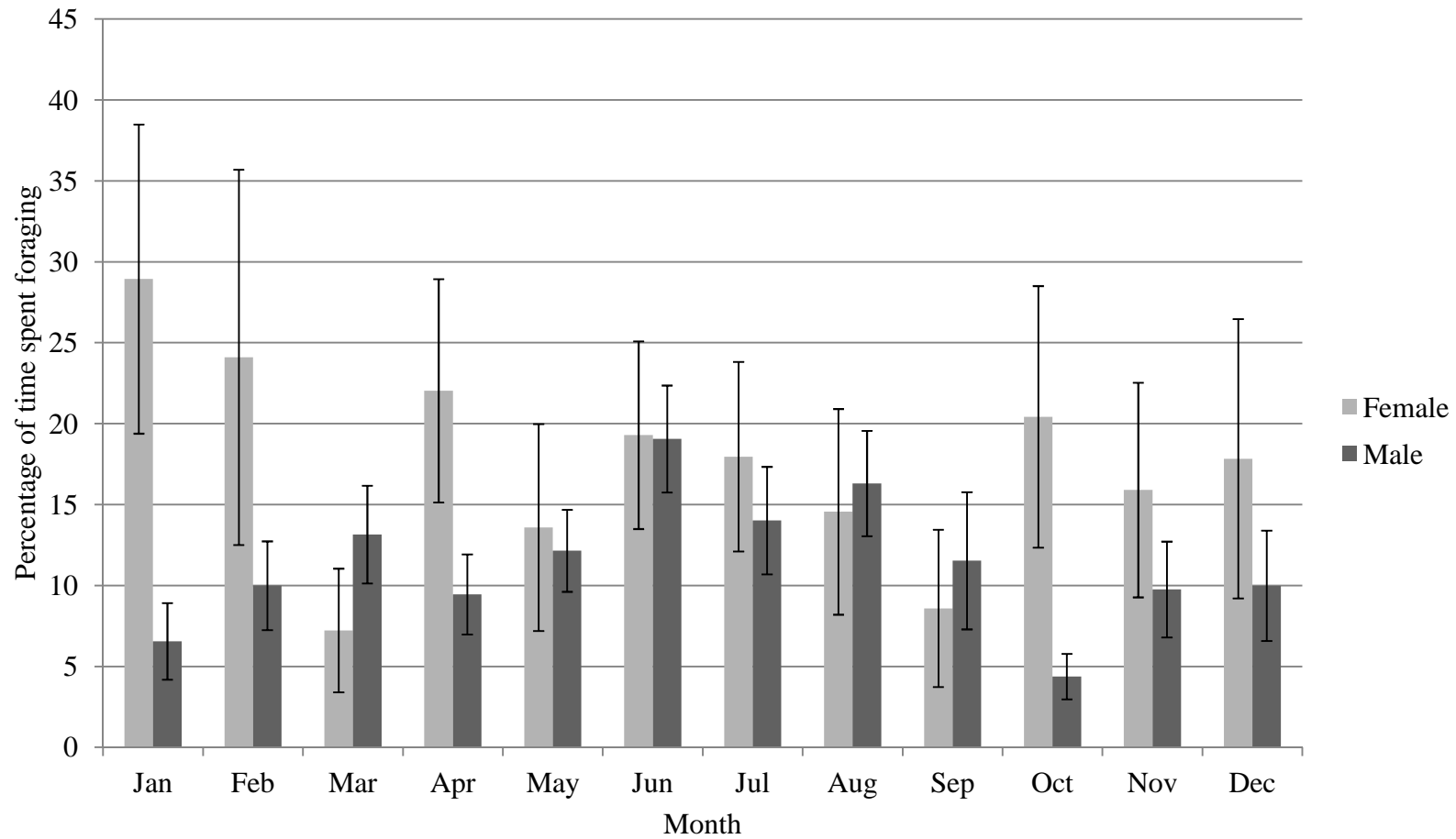
Figure 5. Monthly variation in the percent time ($\bar{x} \pm$ SE) male ($n = 760$ observation sessions) and female ($n = 224$) Hawaiian Ducks spent foraging at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011.

Table 1. Abundance and distribution of diurnal behavioral observation sessions conducted on male and female Hawaiian Ducks in managed wetlands and taro loʻi at Hanalei National Wildlife Refuge, Kauaʻi between September 2010 and August 2011.

Time of day	Sex	Number of observation sessions		
		Managed wetland	Taro loʻi	Total
Early morning	Male	92	99	191
	Female	30	24	54
	n	**122**	**123**	**245**
Late morning	Male	93	94	187
	Female	20	25	45
	n	**113**	**119**	**232**
Afternoon	Male	100	89	189
	Female	22	32	54
	n	**122**	**121**	**243**
Evening	Male	103	90	193
	Female	32	39	71
	n	**135**	**129**	**264**
Grand total		**492**	**492**	**984**

Table 2. Relative frequency of occurrence (%) of foraging behaviors exhibited by Hawaiian Ducks using managed wetlands (n = 208 observation sessions; 18.3 hr) and taro lo'i (n = 151; 24.6 hr) at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011. Behaviors occurring less than 1.0% of the time were listed as trace (tr).

Foraging behavior	Relative frequency of occurrence (%) of foraging behaviors		
	Managed wetlands	Taro lo'i	Overall
Dabble	29.5	32.0	30.9
Head-dip	44.1	56.1	51.0
Up-end	2.7	tr	1.3
Probe	13.9	3.8	8.1
Nibble vegetation	4.3	1.4	2.7
Peck	tr	tr	tr
Snatch/snap	tr	--	tr
Manipulate food	tr	tr	tr
Search	3.9	4.5	4.2
Other	tr	tr	tr

Table 3. Comparisons of the percent time ($\bar{x} \pm$ SE) that Hawaiian Ducks spent in six behavioral categories in managed wetlands ($n = 492$ observation sessions) and taro lo'i ($n = 492$) at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011.

| Behavior | Percent time spent per behavior | | Test statistic value[a] | P-value |
	Managed wetland	Taro lo'i		
Forage	11.1 ± 1.0	15.0 ± 1.3	4.59 [KW]	0.032
Rest	26.8 ± 1.4	44.3 ± 1.6	56.50	< 0.001
Maintenance	28.3 ± 1.2	21.3 ± 1.0	21.25	< 0.001
Locomotion	22.0 ± 1.1	7.5 ± 0.4	148.90	< 0.001
Alert	10.6 ± 0.6	11.4 ± 0.6	0.74	0.388
Social	1.3 ± 0.2	0.5 ± 0.1	11.88 [KW]	< 0.001

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

Table 4. Correlations between foraging behaviors of Hawaiian Ducks and habitat characteristics in managed wetlands at Hanalei National Wildlife Refuge, Kaua'i between September 2010 and August 2011 ($n = 452$ observation sessions).

Habitat variable	Spearman correlation coefficients (r)				
	Forage	Dabble	Head-dip	Nibble Vegetation	Probe
Emergent vegetation height	-0.22[***]	-0.15[**]	-0.15[**]	-0.07	-0.21[***]
Water depth	-0.12[*]	-0.06	-0.03	0.01	-0.1[*]
Total vegetation cover	0.05	0.04	-0.09	0.07	0.14[**]
Cover by select species:					
Cyperus spp.	0.18[***]	0.11[*]	0.04	0.11[·]	0.16[**]
Fimbristylis miliacea	0.17[**]	0.15[**]	0.02	0.14[*]	0.16[**]
Ludwigia octovalvis	-0.23[***]	-0.17[**]	-0.14[*]	-0.06	-0.18[**]
Urochloa mutica	-0.15[**]	-0.12[*]	-0.15[**]	-0.04	-0.05
Echinochloa crus-galli	0.07	0.03	0.02	0.15[*]	-0.02
Paspalum urvillei	0.02	-0.01	0.09	0.08	-0.16[**]

Significance of Spearman correlation analyses with Benjamini-Hochberg correction are indicated by superscripts; [***] $P < 0.001$, [**] $0.001 \leq P < 0.01$, [*] $0.01 \leq P < 0.05$, [·] $0.05 \leq P < 0.10$.

Table 5. Diurnal variation in time-activity budgets ($\bar{x} \pm$ SE) of Hawaiian Ducks using managed wetlands ($n = 492$ observation sessions) and taro loʻi ($n = 492$) at Hanalei National Wildlife Refuge, Kauaʻi from September 2010 through August 2011.

| Habitat | Behavior | Percent time spent per behavior | | | | Test statistic value[a] | P-value |
		Early morning	Late morning	Afternoon	Evening		
Managed wetland	Forage	19.0 ± 2.4 B, C, D	7.3 ± 1.7 A, (D)	6.4 ± 1.5 A, D	11.4 ± 1.9 A, C, (B)	29.35 KW	< 0.001
	Rest	14.8 ± 2.0 B, C, D	34.5 ± 3.3 A	30.6 ± 3.0 A	27.8 ± 2.6 A	8.03	< 0.001
	Maintenance	26.8 ± 2.1	33.2 ± 2.8 D	31.3 ± 2.8	22.8 ± 2.0 B	3.39	0.018
	Locomotion	25.2 ± 2.0 B, C	17.5 ± 2.2 A, D	20.2 ± 2.3 A, D	24.3 ± 2.0 B, C	6.31	< 0.001
	Alert	12.4 ± 1.3 B, C	7.0 ± 0.8 A, D	9.9 ± 1.3 A, D	12.4 ± 1.0 B, C	8.05	< 0.001
	Social	1.7 ± 0.4 B	0.5 ± 0.1 A, C, D	1.6 ± 0.6 B	1.2 ± 0.3 B	10.91 KW	0.012
	n	122	113	122	135		
Taro loʻi	Forage	18.0 ± 2.8 B	7.5 ± 1.9 A, D	13.5 ± 2.6 (D)	20.5 ± 2.8 B, (C)	14.81 KW	0.002
	Rest	32.4 ± 3.0 B, C, (D)	53.9 ± 3.0 A, D	50.9 ± 3.2 A, D	40.6 ± 3.2 B, C, (A)	10.16	< 0.001
	Maintenance	27.0 ± 2.2 D, (C)	21.6 ± 2.1	18.9 ± 2.1 (A)	17.8 ± 1.9 A	4.40	0.005
	Locomotion	9.0 ± 1.0 (B)	5.6 ± 0.8 (A, D)	6.6 ± 0.8	8.5 ± 0.9 (B)	2.90	0.035
	Alert	12.9 ± 1.3 (C)	11.0 ± 1.4	9.6 ± 1.0 (A, D)	11.9 ± 1.1 (C)	2.72	0.044
	Social	0.5 ± 0.2	0.4 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	1.08 KW	0.783
	n	123	119	121	129		

[a] Test statistics are F-values from separate ANOVAs after accounting for sex, pair status, and month unless otherwise indicated; KW Kruskal-Wallis H-values. Multiple comparison tests with a Benjamini-Hochberg correction indicate significant differences ($P < 0.05$) between time periods with superscripts (A = early morning, B = late morning, C= midday, and D = evening); superscripts in parentheses represent marginally significant differences ($0.05 \leq P < 0.10$).

Table 6. Sex-specific differences in time-activity budgets ($\bar{x} \pm$ SE) of Hawaiian Ducks (n_{male} = 760 observation sessions; n_{female} = 224) in two primary habitat types at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011.

Habitat	Behavior	Percent time spent per behavior		Test statistic value[a]	P-value
		Male	Female		
Managed wetland	Forage	10.3 ± 1.1	14.2 ± 2.5	2.59 KW	0.108
	Rest	25.0 ± 1.6	33.7 ± 3.2	5.18	0.023
	Maintenance	28.4 ± 1.4	27.9 ± 2.6	0.16	0.688
	Locomotion	24.1 ± 1.3	14.0 ± 1.6	8.46	0.004
	Alert	10.8 ± 0.7	9.5 ± 1.2	1.08	0.299
	Social	1.5 ± 0.2	0.5 ± 0.1	3.81 KW	0.051
	n	388	104		
Taro lo'i	Forage	13.3 ± 1.4	20.4 ± 3.1	2.63 KW	0.105
	Rest	45.5 ± 1.8	40.6 ± 3.4	< 0.01	0.979
	Maintenance	20.4 ± 1.1	24.1 ± 2.6	3.84	0.051
	Locomotion	7.7 ± 0.5	6.7 ± 0.8	4.47	0.035
	Alert	12.5 ± 0.7	7.9 ± 0.8	10.93	0.001
	Social	0.6 ± 0.1	0.3 ± 0.1	2.34 KW	0.126
	n	372	120		
Overall	Forage	11.8 ± 0.9	17.5 ± 2.0	4.99 KW	0.026
	Rest	35.0 ± 1.2	37.4 ± 2.4	1.93	0.165
	Maintenance	24.4 ± 0.9	25.9 ± 1.8	1.92	0.166
	Locomotion	16.1 ± 0.8	10.1 ± 0.9	11.58	< 0.001
	Alert	11.7 ± 0.5	8.6 ± 0.7	9.28	0.002
	Social	1.0 ± 0.1	0.4 ± 0.1	6.57 KW	0.010
	n	760	224		

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

Table 7. Comparison of activity budgets ($\bar{x} \pm$ SE) between paired ($n = 193$ observation sessions) and unpaired ($n = 513$) Hawaiian Ducks using managed wetlands and taro loʻi at Hanalei National Wildlife Refuge, Kauaʻi from September 2010 to August 2011.

| Habitat | Behavior | Percent time spent per behavior | | Test statistic value[a] | P-value |
		Paired	Unpaired		
Managed wetland	Forage	14.6 ± 2.4	11.0 ± 1.3	1.07 [KW]	0.301
	Rest	27.8 ± 3.2	24.0 ± 1.8	0.75	0.388
	Maintenance	26.3 ± 2.4	28.6 ± 1.7	0.65	0.421
	Locomotion	17.0 ± 1.8	24.5 ± 1.5	3.00	0.084
	Alert	11.8 ± 1.2	10.8 ± 0.8	0.27	0.601
	Social	2.6 ± 0.7	1.1 ± 0.2	3.57 [KW]	0.059
	n	105	260		
Taro loʻi	Forage	27.1 ± 3.8	13.0 ± 1.7	13.98 [KW]	< 0.001
	Rest	35.3 ± 3.9	47.4 ± 2.2	9.47	0.002
	Maintenance	18.9 ± 2.4	21.4 ± 1.4	3.08	0.080
	Locomotion	8.3 ± 1.1	6.9 ± 0.6	6.18	0.013
	Alert	9.6 ± 1.4	11.1 ± 0.8	0.99	0.321
	Social	0.9 ± 0.2	0.3 ± 0.05	5.81 [KW]	0.016
	n	88	253		
Overall	Forage	20.3 ± 2.2	12.0 ± 1.1	11.39 [KW]	< 0.001
	Rest	31.2 ± 2.5	35.5 ± 1.5	2.88	0.090
	Maintenance	22.9 ± 1.7	25.0 ± 1.1	4.38	0.037
	Locomotion	13.1 ± 1.2	15.8 ± 0.9	0.10	0.749
	Alert	10.8 ± 0.9	10.9 ± 0.6	1.22	0.270
	Social	1.8 ± 0.4	0.7 ± 0.1	9.43 [KW]	0.002
	n	193	513		

[a] Test statistics are *F*-values from separate ANOVAs after accounting for time of day, month, and sex unless otherwise indicated; [KW] Kruskal-Wallis *H*-values.

DISCUSSION

THE BEHAVIORAL REPERTOIRE AND SOCIAL INTERACTIONS OF HAWAIIAN DUCK

While previous observations have partially described social behaviors of Hawaiian Duck (Johnsgard 1965, Weller 1980, Engilis et al. 2002), this study provides a more complete account of Hawaiian Duck behavioral repertoire and is the first to quantify their specific behavioral activities. Similar to other insular, endemic dabbling ducks of the Pacific, the phylogeny of the Hawaiian Duck has been variable and debatable (Lack 1970, Weller 1980, Livezey 1991, 1993, Browne et al. 1993, Rhymer 2001); however, there is general agreement that Hawaiian Duck is a close relative of the Laysan Duck (*Anas laysanensis*), Mallard and North American allies within the Mallard complex that includes the Mottled Duck (*A. fulvigula*) and Mexican Duck (*A. platyrhynchos diazi*; Browne et al. 1993, Rhymer 2001). Thus, this group of *Anas* species serves as the best direct comparison with Hawaiian Duck. Consistent with our prediction, we found that the behavioral repertoire of the Hawaiian Duck was similar to that of the well-described Mallard (Lorenz 1951, Johnsgard 1965, McKinney 1965, Johnsgard 1975, Drilling et al. 2002).

Unlike the Laysan Duck that exhibits novel terrestrial foraging behaviors (e.g., Brine fly [*Scatella sexnotata*] chasing, "dive-bomb" fly-catching) to exploit seasonally abundant food sources (Warner 1963, Reynolds 2002), the Hawaiian Duck did not display any unique foraging behaviors, and observations at Hanalei NWR indicate that the Hawaiian Duck uses the same repertoire of foraging tactics as those described for the Mallard and Mottled Duck (Goodman and Fisher 1962, Johnsgard 1965, Kear and Johnsgard 1968, Paulus 1984b, Stutzenbaker 1988, Drilling et al. 2002). While both the Hawaiian Duck and Laysan Duck have developed clear morphological differences with Mallard (e.g., body size, pelvic dimensions, plumage; Livezey 1993, Engilis et al. 2002), these changes have not accompanied a discernible alteration of the fundamental foraging behaviors of Hawaiian Duck. Livezey (1993) proposed that the comparatively long tarsometatarsus and middle toe and short tibiotarsus of Hawaiian Duck developed in response to terrestrial foraging activities, as these pelvic dimensions may improve terrestrial locomotion at the expense of aquatic propulsive power; however, birds at Hanalei NWR exhibited relatively little terrestrial foraging (e.g., <1% of time when on

taro dikes) and fed primarily by head-dipping and dabbling in shallow water. If terrestrial foraging is common in Hawaiian Duck, it occurs at night or in habitats other than lowland wetlands.

While Hawaiian Duck exhibited similar maintenance and resting behaviors to Mallard, Mottled Duck, and Laysan Duck, their locomotor and alert behaviors, particularly response to potential predators, appeared more similar to Mallard than Laysan Duck (McKinney 1965, Johnsgard 1960, Paulus 1984b, Marshall 1989, Reynolds 2002). The Laysan Duck and, until approximately 1,000 years ago, the Hawaiian Duck evolved with avian predators rather than mammalian predators (Olson and James 1982, 1991; Burney et al. 2001); however, the Hawaiian Duck readily takes flight when disturbed or startled, whereas the Laysan Duck often freezes to avoid detection (Marshall 1989, Reynolds 2002). The wing dimensions and carina sterni, which is generally proportional to size of breast muscles, of both these insular species have undergone reduction compared to Mallard; although, the reduction is more pronounced in Laysan Duck (Livezey 1993). These crucial disparities in potential flight ability and behavioral response to predators and disturbance may partially explain why the Hawaiian Duck persisted in the main Hawaiian Islands following Polynesian contact and introduction of mammalian predators, whereas the Laysan Duck disappeared.

The courtship behaviors of Hawaiian Duck were similar to those reported for Mallard, Mottled Duck, and Laysan Duck; however, the form and linkage of these courtship displays slightly differed (Lorenz 1951, Johnsgard 1960, Johnsgard 1965, Weller 1980, Paulus 1988c, Moulton and Weller 1984). Typical of *Anas,* Hawaiian Duck courtship activity was generally initiated by a series of introductory displays (e.g., head-shaking, head-flicking, body-shaking) by males. Females occasionally performed the nod-swimming display to elicit courtship displays from males. Introductory displays and female nod-swims were generally followed by the grunt-whistle, the head-up-tail-up display, and/or the down-up display by males. The order of these three displays was variable; however, the grunt-whistle occurred most frequently. Weidman (1956) suggested that the grunt-whistle, head-up-tail-up, and down-up in Mallards represented different intensities of courtship behavior, where the grunt-whistle was performed during

low intensity situations, and the head-up-tail-up and down-up were performed during high intensity situations. Likewise, Johnsgard (1960) found that the grunt-whistle was performed more frequently during the early pair formation period of Mallards, whereas the down-up occurred more frequently during peak pair formation months. Similar to Mallard and Mottled Duck (Johnsgard 1965, Paulus 1984a), the head-up-tail-up display of Hawaiian Duck was often linked with nod-swimming. However, unlike the Mallard and Mottled Duck, Hawaiian Duck males performed independent nod-swimming displays, supporting observations made by Johnsgard (1965). Also confirming observations of Johnsgard (1965), the form of nod-swimming by Hawaiian Duck differed slightly from Mallard and Mottled Duck in that Hawaiian Duck tended to nod the head during this display, a variation also exhibited by Laysan Duck.

Other courtship behaviors that may differ from Mallard and Mottled Duck include the jump-flight and dash-and-dive displays. As reported for Mallard (Lebret 1958), Hawaiian Duck males performed jump-flight displays to attract the attention of females. However, unique to Hawaiian Duck, females were also rarely observed performing simultaneous jump-flights with mates. Due to the rarity in which this display was observed, the function of this behavior by females is not clear. Female jump-flights may serve to reinforce pair-bonds or to elicit sexual displays from males, as in nod-swimming. Dashing-and-diving has been described as a form of bathing in some *Anas* species, and this behavior may stimulate others to join bathing (McKinney 1965); however, paired Hawaiian Duck males and females were infrequently observed dashing-and-diving both individually and simultaneously during courtship and post-copulation activities. Other post-copulatory behaviors involved vigorous preening and bathing, nod-swimming, wing flapping, various shakes, and bridling (males only). It was not always clear if these post-copulatory behaviors, including dashing-and-diving, served as display behaviors that strengthened pair-bonds or as normal movements to remove water and rearrange feathers that were displaced during copulation. Based on the vigorous and exuberant nature in which these behaviors were performed, they likely serve a purpose more complicated than the normal maintenance function.

Whether the relative frequency of occurrence of specific male courtship displays differs between Hawaiian Duck and closely related *Anas* is still uncertain. Paulus (1988c), who used similar sampling techniques (i.e., instantaneous focal sampling), found that Mottled Ducks generally allocate comparable proportions of courting time to each of the major displays. However, discrete behavioral events that are rare or of short duration relative to the sample interval (e.g., specific courtship displays) are not adequately measured by this sampling design (Martin and Bateson 2007), and future studies directed at quantifying these rare courtship events would benefit from a continuous sampling approach.

Male Hawaiian Ducks were associated with brood-tending females in 11.3% (19 of 168) of brood observations (Appendix E); however, the function of this behavior is unclear. Male parental care and pair-bond maintenance during brood-rearing has been described for *Anas* of the tropics and Southern Hemisphere (Siegfried 1974, McKinney and Brewer 1989, Sorenson 1992), and Weller (1980) proposed that brood care by males is more common in island endemic species. Yet, for Hawaiian Duck, the rate of mate attendance during brood-rearing is comparatively low, and the relationship of the attending male to the female or brood was unknown. Attending males were often passive, seldom displayed, and provided little defense, which contrasted the typical assiduous mate-guarding behavior of paired males. Similarly, White-cheeked Pintail (*Anas bahamensis bahamensis*) males did not provide direct care for the brood; however, those males followed and occasionally defended their mates and performed pair-bond maintenance displays (Sorenson 1992). Thus, while observations were limited, brood attendance by Hawaiian Duck males seemed primarily to be a male strategy in which females accepted, or at least tolerated, certain attending males, but received little apparent benefit. Given the heavily skewed sex ratio at Hanalei NWR compared to related *Anas* (Bellrose 1980, Moulton and Weller 1984, Reynolds 2002), male attendance may incur certain fitness advantages, such as providing additional breeding attempts after the first brood fledges or fails, or maintaining pair-bonds for the subsequent breeding season. Alternatively, with a subset of females in breeding condition year-round and the opportunity to obtain more than one mate in a given breeding season, males may only

attempt to maintain pair-bonds with brood-tending females until they have the opportunity to switch mates (McKinney 1985, Sorenson 1992, Oring and Sayler 1992). While the Hawaiian Duck appears to be seasonally monogamous (Engilis et al. 2002, Malachowski and Dugger, unpubl. data), concurrent or serial polygyny may occur during the asynchronous and extended breeding season. The mating system, pair-bond dynamics, and the role of male attendance during brood rearing warrants future study.

Similar to the Mallard and Mottled Duck, the Hawaiian Duck allocated minimal time (<1%) to agonistic interactions (Jorde 1981, Paulus 1988c); however, most (90%) interspecific interactions involved aggression towards or submission by the Hawaiian Duck. Also, while often short in duration, these encounters occurred in 13% (131 of 984) of observation sessions, suggesting that even the brief amount of time that Hawaiian Ducks spent interacting with other waterbirds may be significant and could potentially influence Hawaiian Duck behavior and distribution at Hanalei NWR.

In summary, the behavioral repertoire of the Hawaiian Duck appeared similar to that of the Mallard, which is consistent with their close genetic relationship and the absence of strong climatic and ecological pressures that would drive the evolution of a unique set of behaviors. Subtle variations in the form and linkage of certain courtship displays compared to Mallard may reflect ancestral behavioral traits from their divergence from Laysan Duck. While foraging strategies more closely resemble those of Mallard and Mottled Duck, it is not clear if the morphological differences of Hawaiian Duck (e.g. pelvic limb dimensions) would align with similar behavioral plasticity exhibited by Laysan Duck if presented with comparable habitat and resource restrictions as experienced on Laysan Island.

HAWAIIAN DUCK BEHAVIOR AND RESPONSE TO WETLAND HABITAT MANAGEMENT AND TARO CULTIVATION

Effects of habitat type and wetland characteristics

Hawaiian Ducks allocated diurnal activity budgets differently in managed and cultivated wetland habitat at Hanalei NWR. Birds used taro loʻi and dikes primarily for foraging and resting, whereas birds utilized managed wetlands for a variety of requirements, including maintenance, rest, food, and courtship. The increased range of activities

performed in managed wetlands may reflect the greater habitat diversity provided by 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. While birds spent slightly more time foraging when using taro, the difference seems of minimal biological consequence, and it is not clear how waterfowl food diversity and production varies between habitat types at Hanalei NWR.

While the relationship was weak, Hawaiian Ducks spent more time foraging in managed wetland units that contained more *F. littoralis* and *Cyperus* cover. *F. littoralis* was abundant in most wetland units, but cover was highest in early successional wetlands. These moist-soil plant species provide high seed production, important nutrient sources (e.g., carbohydrates and protein; DesRochers et al. 2010), and are among the species targeted by wetland management at Hanalei NWR (Smith 2011). Birds were observed nibbling seed heads of several emergent wetland plant species, such as *F. littoralis*, *E. crus-galli*, *C. javanicus*, and *C. polystachyos*. In addition to seed production, wetland plants, such as *F. littoralis* and *E. crus-galli*, provide cover and roosting habitat, as well as important structure for aquatic invertebrates, such as Chironomidae (e.g., midges), Astacidea (e.g., crayfish), and Mollusca (e. g., snails), which may be a valuable source of proteins and lipids for Hawaiian Duck (Smith 2011, Engilis 2002). Additionally, the relatively rapid vegetative breakdown of these plants also promotes conditions (i.e., habitat and nutrients) for invertebrate growth (Smock and Stoneburner 1980, Magee 1993, Smith 2011), and observations of foraging behavior suggest that birds probed in matted vegetation, particularly *F. littoralis*, and soil to access invertebrates and seeds.

Among taro cover classes, Hawaiian Ducks allocated the greatest proportion of time to foraging when using harvested loʻi; 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) that includes taxa reported in the diet of Hawaiian Duck (Henshaw 1902, Perkins 1903, Schwartz and Schwartz 1953, Munro 1944, Engilis et al. 2002). In addition, Hawaiian Duck were observed feeding on

Chlorophyceae (filamentous green algae), *L. aequinoctialis* (lesser duckweed), and *A. filiculoides* (large mosquito fern) which were abundant in many loʻi and possibly linked to large nutrient influxes associated with fertilizer applications. The greater foraging effort in harvested taro may reflect greater availability of aquatic invertebrates due to soil disturbance associated with foot action by farmers and the accumulation of large amounts of residual plant material, which provides structure and food for invertebrates. While behavioral observations provide initial information on Hawaiian Duck use of taro, a more complete understanding of the relative value of various taro cover classes could be achieved through studies that assess diet and habitat selection of Hawaiian Ducks across the annual cycle.

As predicted, Hawaiian Ducks generally allocated less of their diurnal activity budget to foraging (13%) than North American *Anas* species (e.g., Kaminski and Prince 1981, Paulus 1984b, Paulus 1988a, Turnbull and Baldassarre 1987). For example, Mottled Ducks spent 39% and 53% of daytime feeding during non-breeding and breeding seasons, respectively; however foraging time varied substantially depending on month, stage of the breeding cycle, and sex (Paulus 1984b). Although mean monthly foraging by Hawaiian Ducks ranged from 4 to 19% for males and 7 to 29% for females, time spent foraging is generally lower and less variable than Mallards in North America, which spend 7-64% of daytime feeding in wetlands (Dwyer et al. 1979, Kaminski and Prince 1981, Turnbull and Baldassarre 1987, Dugger and Petrie 2000, Johnson and Rohwer 2000). Given Hawaiian Duck have an approximately 50% smaller body size and mass than Mallard, our results seem inconsistent with the body size hypothesis, in which smaller bodied species have higher mass-specific metabolic rate and allocate more time to feeding (Calder 1996, Gloutney et al. 2001); however, food intake rate was not measured. Instead, the relatively large disparity in foraging time between Hawaiian Ducks and North American *Anas* might suggest that Hawaiian Ducks have lower daily and seasonal energy demands associated with mild climate and sedentary lifestyle, allocate a greater amount of time to nocturnal foraging activities, or have access to higher quality diet or greater food availability.

Whereas Hawaiian Ducks generally spent less time foraging than closely related *Anas*, they allocated relatively more time to diurnal maintenance, alert, and locomotor behaviors. For example, maintenance behaviors accounted for 9% of Mottled Duck diurnal activity budgets (Paulus 1984b) and generally less than 13% of Mallard activities in wetlands (Kaminski and Prince 1981, Turnbull and Baldassarre 1987, Dugger and Petrie 2000); however, Hawaiian Ducks spent 25% of the time in these behaviors. Also, Hawaiian Ducks tended to exhibit slightly more alert behavior (11%) than Mottled Ducks (8%; Paulus 1984b, Paulus 1988b) and Mallards (2-6%; Kaminski and Prince 1981, Turnbull and Baldassarre 1987, Dugger and Petrie 2000). Increased maintenance and alert behavior in Hawaiian Ducks relative to these North American *Anas* might be explained by lower energy demands and the opportunity to allocate diurnal activities to those other than foraging. Elevated alert activities compared to Mallard and Mottled Duck may also correlate with higher levels of human disturbance (i.e., farmer and USFWS activities; Appendix K, L), smaller wetland patch sizes, which make disturbances more difficult to avoid, or increased risk of predation, as birds with smaller body sizes may be more susceptible to avian predation (McWilliams et al. 1994).

Overall, Hawaiian Ducks spent 36% of the time resting, which is similar or slightly higher than the diurnal values reported for nonbreeding (36%; Paulus 1988b) and breeding (24%, Paulus 1984b) Mottled Duck. Mallards exhibit substantially more variability in resting activity depending on season, year, geographic location, and habitat (8-54%; Kaminski and Prince 1981, Turnbull and Baldassarre 1987, Dugger and Petrie 2000). Hawaiian Ducks allocated significantly more time to rest when in taro than when in managed wetlands, and like Mallards and Mottled Ducks (Drilling et al. 2002, Paulus 1984b), Hawaiian Ducks typically rested on land. While Hawaiian Ducks loafed in open water, on tufts and islands of matted vegetation (e.g., *F. littoralis*), and under emergent wetland vegetation canopy (e.g., taro, *L. octovalvis*), birds were most frequently observed resting on the dikes of taro lo'i that crisscross the Hanalei NWR landscape. Similar to previous surveys (Gee 2007, Gutscher-Chutz 2011), 61% of 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 aides in predator detection, and quick access to escape cover.

Courtship activities accounted for less than 1% of Hawaiian Duck activity budgets, but occurred significantly more frequently in managed wetlands than in taro. Data on courtship habitat requirements are rare for anatids; however, Weeks (1969) found that within wetlands Mottled Ducks most often used small pockets of open water surrounded by dense vegetation or water areas between vegetated islands for courtship. Also, Heitmeyer (1985) determined that Mallards most often used shrub-scrub wetlands in Missouri and suggested that habitat might be preferred as it provided greater protection from predators. I suspect that increased levels of courtship activity by Hawaiian Duck in managed wetlands were attributed to a variety of factors, such as overall wetland size, vegetation structure and distribution, and water depth. Wetland units at Hanalei NWR were generally larger than taro loʻi and had a hemi-marsh structure where pockets of open water were interspersed amongst emergent wetland vegetation, which may provide cover from avian predators.

Daily and seasonal variation in behavior

In addition to habitat type, the most important factor influencing the activity patterns of Hawaiian Duck at Hanalei NWR was time of day. Primarily, Hawaiian Ducks foraged more and rested less during early morning and evening than late morning and afternoon. Since more birds occurred at Hanalei NWR during the evening and early morning than other times of day (Appendix O), activity budget data suggests that refuge wetlands provide valuable foraging habitat for Hawaiian Ducks on Kauaʻi. While a subset of the Hawaiian Duck population likely uses Hanalei NWR throughout the day, large numbers of birds were observed flying to refuge wetlands from adjacent wetlands and river valleys during the evening (Malachowski, pers. obs.). Foraging and locomotor activity increased during this period and remained high during the early morning. Hawaiian Duck abundance then decreased sharply during late morning, and birds remaining at Hanalei exhibited a lull in foraging and social activity and increased time spent resting. Variation in the timing of activity patterns is common for many North American Anatids (Paulus

1988a). For example, peak diurnal foraging activity of Mottled Ducks occurs during early morning; however, several studies indicate that Mottled Ducks and other *Anas* species, such as Laysan Duck, American Black Duck (*A. rubripes*), Gadwall (*A. strepera*), and Green-winged Teal, may spend less overall time feeding diurnally than nocturnally (Tamisier 1974, Paulus 1984a, 1988b, Reynolds 2002, Jones III 2012). Quantifying nocturnal behavioral activities would help complete the picture of Hawaiian Duck activity budgets.

While Hawaiian Ducks demonstrated generally consistent patterns of daily behavioral activities, the mechanisms for explaining these patterns are unclear. The timing and allocation of daily activities of dabbling ducks can be driven by a variety of abiotic and biotic factors, including thermal conditions (e.g., extreme cold or heat; Calder and King 1974, Jorde et al. 1984, Paulus 1988b, Turnbull and Baldassarre 1987, Reynolds 2002), resource availability (e.g., aquatic insect emergence, tidal stage; Swanson 1977, Pietz and Buhl 1999, Johnson and Rohwer 2000), disturbances (Dimond and Lazarus 1974, Pöysä 1998), and risk of avian predation (Tamisier 1974, Pöysä 1987, Dekker 1987). For instance, the relatively low proportion of time spent foraging by Hawaiian Ducks during late morning and afternoon hours could represent an attempt to avoid heat stress and UV exposure by resting and remaining under cover (Reynolds 2002). Alternatively, variation in the timing of diurnal activity patterns may be influenced by human disturbances or intraspecific and interspecific aggression and competition at Hanalei NWR.

Consistent with my prediction, and unlike many North American migratory waterfowl, the Hawaiian Duck population using Hanalei NWR did not exhibit a strong seasonal pattern in most behaviors. This may reflect their non-migratory nature and the mild yearly climate. For example, North American waterfowl considerably increase their foraging in preparation for migration and in extreme climate (Miller 1985, McLandress and Raveling 1981, Jorde et al. 1984, Paulus 1988b). Alternatively, it is possible that seasonality was not detected because nocturnal foraging increased during certain times of the year corresponding with energetically costly life history events. However, it is also likely that the comparatively asynchronous life-history cycle of Hawaiian Duck made

important variation in individual behavior associated with each life-history stage difficult to detect since individuals of any life-history stage could occur at any given time, and I was unable to assign birds to a life-history stage when they were observed.

While strong seasonal patterns were not detected in time allocated to foraging by Hawaiian Duck, birds exhibited seasonal shifts in the relative use of foraging tactics. Hawaiian Ducks probed for food items more frequently during July and August than other months, suggesting a seasonal shift in targeted prey items which may align with food abundance and availability or life-history specific (e.g., molting) dietary requirements. Alternatively, seasonal fluctuations in water levels may expose probing substrates; however, foraging behaviors were not strongly correlated with water depth (Table 4).

Males exhibited increased vigilance, courtship, and mate-guarding behavior during months generally associated with peak pair-formation (i.e., November to March). These patterns suggest that although Hawaiian Duck have staggered life-history cycles and breed year-round, birds using Hanalei NWR had subtle seasonality of the annual cycle with courtship and pair-formation occurring more often between November and March. Similar to other *Anas*, many Hawaiian Duck pairs formed just prior to months with peak courtship behavior (Fig. 3, Fig. 4), which suggests pairs re-formed bonds that originated during previous years or birds paired with more subtle and less visible courtship displays (Paulus 1984a, Paulus 1988c, McKinney 1992). As the number of available females decreases, courting parties may escalate in size and courting activities may increase in frequency, intensity, and visibility (McKinney 1992). Consistent with the evidence that peak pair-formation occurs during November to March, the estimated nest initiation date for 70% of unique broods ($n = 67$) observed at Hanalei NWR was between December and May (Appendix E). However, despite the apparent peak in breeding during these months, the proportion of paired females remained high throughout the year ($62.4 \pm 5.6\%$, excluding juveniles and females with broods), suggesting that Hawaiian Ducks maintain extended seasonal pair bonds, which may afford females increased dominance ranking and access to higher quality resources (Paulus 1983, Heitmeyer 1985) or additional opportunities to renest.

Time allocated to interspecific agonistic interactions with other waterbirds was generally low; however, Hawaiian Duck spent nearly twice as much time engaged in these activities between April and July (0.23 ± 0.03%) than other months (0.12 ± 0.02%), and Hawaiian Duck were consistently the recipients of aggression. I suspect that this pattern of interspecific interactions may be linked to seasonal shifts in waterbird abundance, breeding activity, and territoriality. For example, during at least a portion of April to July, the Hawaiian Moorhen, Hawaiian Coot, Hawaiian Stilt, and Hawaiian Goose were nesting or raising young. The aggressive nature and heightened level of territoriality of these waterbirds during this period may have led to increased aggression towards the Hawaiian Duck and possibly influenced daily habitat use and activity patterns of Hawaiian Duck on the refuge (Robinson et al. 1999, Banko et al. 1999, Bannor and Kiviat 2002, Pratt and Brisbin Jr. 2002, USFWS 2011). However, the concept of an interspecific dominance hierarchy among the entire suite of endangered Hawaiian waterbirds in regards to resource competition (e.g., food and loafing habitat), density dependence, and successful brood-rearing has not been investigated.

Effects of sex and pair status

Sex and pair status also affected the activity budgets of Hawaiian Ducks. While the change in female foraging activity was not statistically significant on a monthly or seasonal basis, there was evidence of disproportional foraging activity among sexes, particularly between October and April when females allocated twice as much time to foraging than males (Fig. 5). Male and female North American *Anas*, such as Mallards and Mottled Ducks, generally allocate similar proportions of time to foraging, except during the breeding season when females experience a higher nutrient demand (Dwyer et al. 1979, Drobney 1980, Jorde 1981, Paulus 1984b, Turnbull and Baldassarre 1987, Krapu and Reinecke 1992). This pattern of sex-specific differences in foraging activity of Hawaiian Ducks is consistent with the seasonality suggested by peaks in courtship and pair formation between November and March. Also, the higher nutrient demand of reproductively active females could partially explain why paired female Hawaiian Ducks allocated significantly more time to feeding than unpaired females. Alternatively, among

North American Anatids, access to higher quality habitat is often influenced by an intraspecific dominance hierarchy, and paired birds generally dominate unpaired birds (Raveling 1970, Alexander and Hair 1979, Paulus 1983, Hepp and Hair 1984). Females would, therefore, benefit from mate-guarding and vigilance provided by a mate, and the highly skewed sex ratio in favor of males at Hanalei may allow females to garner extended male care, which might explain the high mean monthly proportion of paired Hawaiian Duck females throughout the year (62%). These patterns also suggest that males may forego feeding to obtain and defend mates, thereby protecting paternity and providing mates with the opportunity to increase foraging time (Ashcroft 1976, Jorde 1981, Krapu and Reinecke 1992).

In summary, behavioral activities of Hawaiian Duck differed between habitat types, time of day, seasons, sexes, and social status. As predicted, Hawaiian Duck demonstrated increased courtship behavior between November and March, which suggests subtle seasonality of the annual cycle. In addition, females allocated more time to foraging than males, particularly during months that may correspond with breeding. Results also suggest that both managed wetlands and taro contribute to fulfilling daily and seasonal resource requirements for Hawaiian Duck. Swedberg (1967) noted that all the Hawaiian Duck's necessary habitat requirements (i.e., forage, loafing and roosting areas, nesting or molting cover) are seldom fulfilled within one location. As a result, Hawaiian Duck will likely use more than one habitat on a daily basis (Perkins 1903, Swedberg 1967, Shallenberger 1977, Giffin 1983). Likewise, Mottled Ducks and Mallards often make regular movements between habitat types used for different activities (Jorde 1981, Jorde et al. 1984, Paulus 1988a, Heitmeyer 1985, Paulus 1988b, Drilling et al. 2002). A more complete understanding of Hawaiian Duck activity budgets and behavioral ecology would benefit from telemetry studies that characterize daily and seasonal movement patterns and relative habitat use on Kaua'i, as well as studies that quantify nocturnal behavior.

Management implications

Daily and seasonal activity budgets suggest that both managed wetlands and taro contribute to fulfilling resource requirements of Hawaiian Duck; however, the increased range of activities performed in managed wetlands suggests that greater habitat diversity is provided by seasonal wetland systems. Dikes around taro loʻi provide important diurnal loafing habitat for Hawaiian Ducks using taro habitat. In addition, our results support management objectives to target *Cyperus* spp. and *Fimbrystis* spp. as forage for Hawaiian Duck. Nevertheless, in the absence of data on habitat-specific differences in food availability and production between managed wetlands and taro, it is difficult to assign relative value to each habitat type for foraging Hawaiian Ducks. Future research should investigate Hawaiian Duck foraging ecology and habitat-specific food availability.

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. Results suggest this management strategy is appropriate because Hawaiian Duck lacked strong seasonal shifts in activity budgets and breeding activity was observed year-round. However, the subtle degree of seasonality suggested by peak courtship, pair formation, and brood observation may help refine the timing of predator control activities. While predator control is recommended year-round, it may be disproportionately important during peak breeding when nesting females and broods are vulnerable.

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APPENDICES

Appendix A. Monthly precipitation at Princeville Ranch, approximately one km north of Hanalei National Wildlife Refuge, Kaua'i.
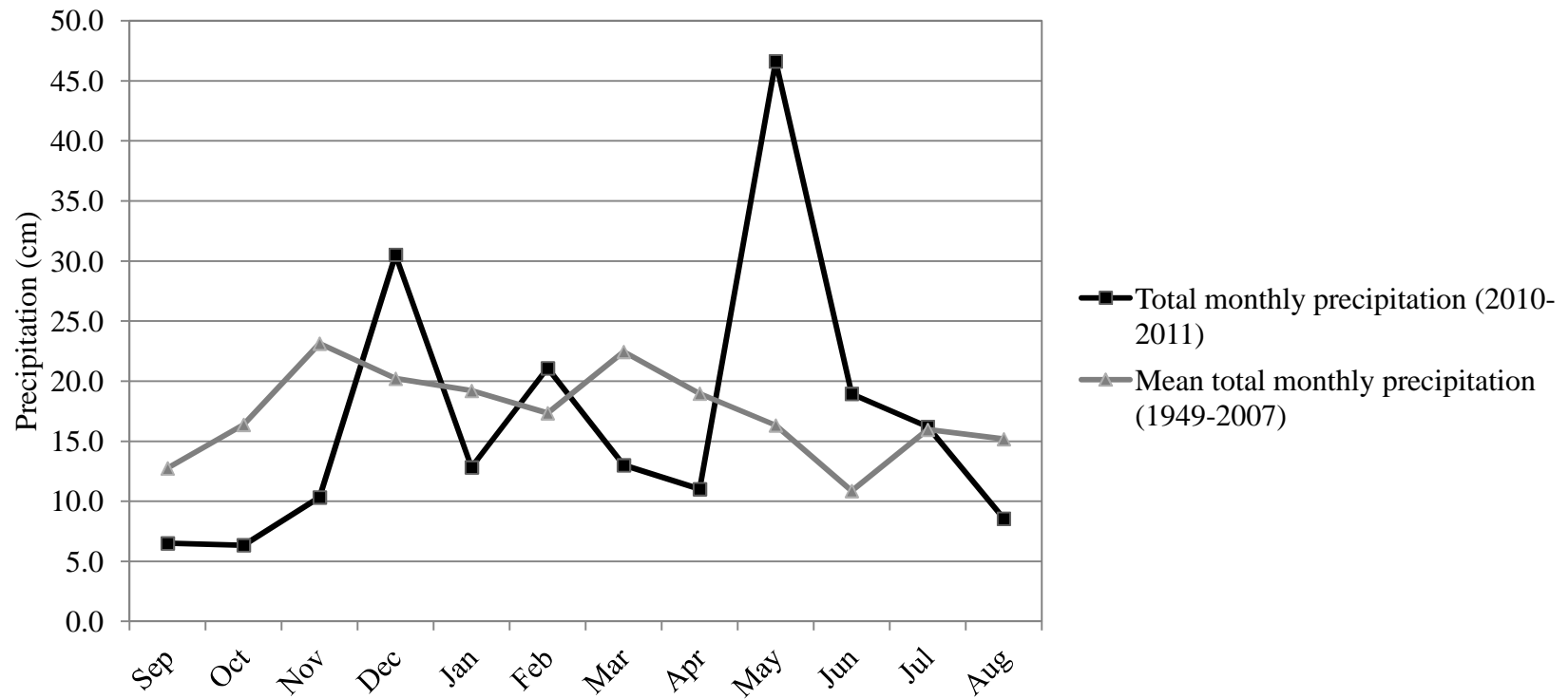
Appendix B. Monthly mean temperatures (°C) at Princeville Ranch, approximately one km north of Hanalei National Wildlife Refuge, Kauaʻi.
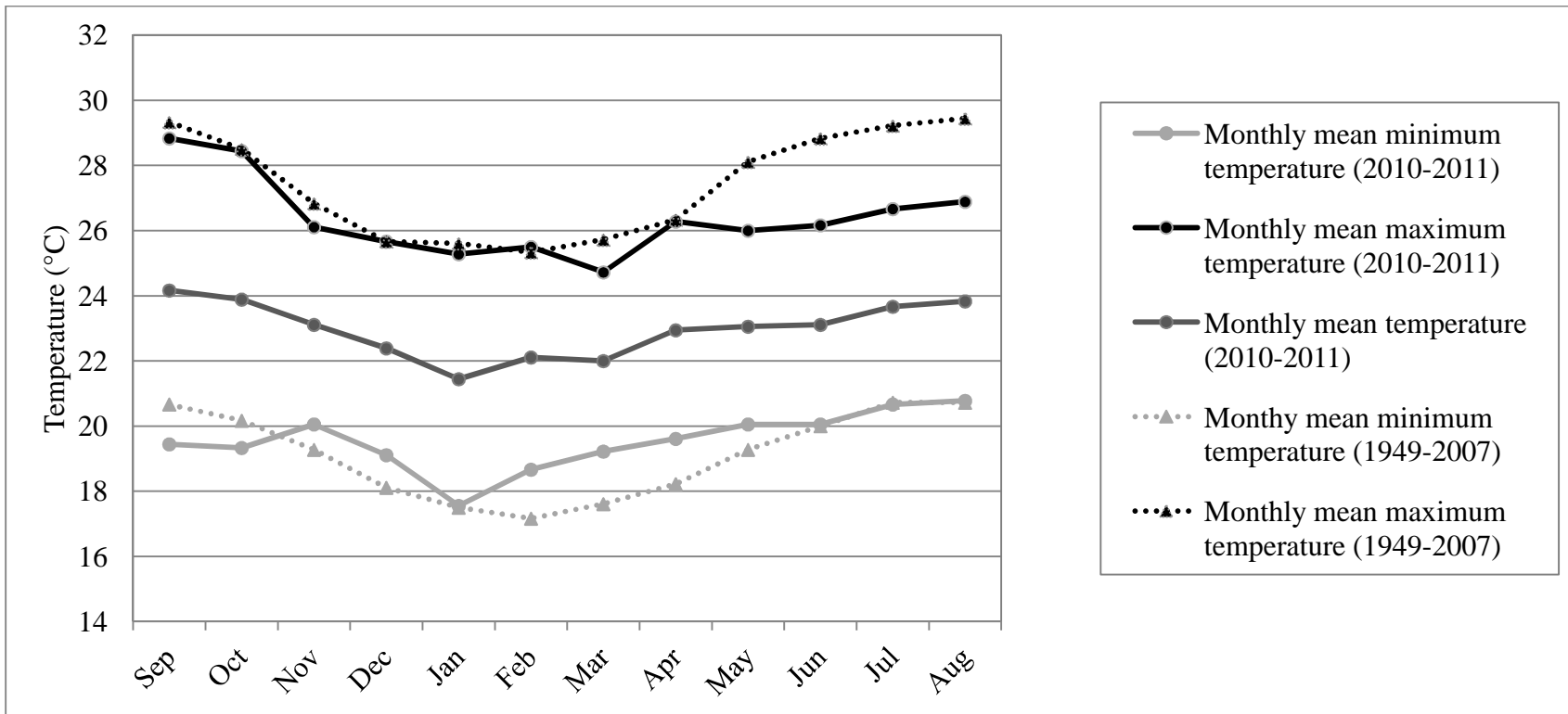
Appendix C. Area (ha) of managed wetland units (mw) and taro loʻi (loʻi) study sites at Hanalei National Wildlife Refuge, Kauaʻi.

Unit ID	Unit type	Area (ha)	Complex area (ha)	Unit ID	Unit type	Area (ha)	Complex area (ha)
A1	mw	1.22	1.22	K25	loʻi	0.14	1.23
B3	mw	1.98	1.98	K26	loʻi	0.27	
B4	mw	1.71	1.71	F21	loʻi	0.10	
C2	mw	2.52	2.52	F22	loʻi	0.23	
DU2	mw	3.26	3.26	F23	loʻi	0.19	
RM1	mw	0.31	0.83	F24	loʻi	0.31	
RM2	mw	0.26		K30	loʻi	0.28	1.41
RM3	mw	0.27		K31	loʻi	0.20	
D1	loʻi	0.26	1.02	K32	loʻi	0.22	
D2	loʻi	0.32		K33	loʻi	0.23	
D17	loʻi	0.20		K34	loʻi	0.21	
D18	loʻi	0.25		K35	loʻi	0.27	
D19	loʻi	0.37	1.37	S15	loʻi	0.14	0.85
D20	loʻi	0.44		S16a	loʻi	0.09	
D21	loʻi	0.36		S16b	loʻi	0.10	
D26	loʻi	0.21		S19	loʻi	0.09	
H46	loʻi	0.34	1.55	S20	loʻi	0.10	
H47	loʻi	0.22		S24	loʻi	0.11	
H52	loʻi	0.49		S25	loʻi	0.10	
H53	loʻi	0.21		S28	loʻi	0.13	
H58	loʻi	0.30					

Appendix D. Hawaiian Duck behavioral activities and descriptions. Terminology
adopted from Lorenz (1951), McKinney (1965), and Johnsgard (1965).

Behavior	Description
Forage	
Dabble	Filter feeding from the water or mud
Head-dip	Submerging head and/or neck to forage
Up-end	Pivoting downward while floating on the surface to reach food items at or near the bottom
Dive	Up-ending and submerging entire body to reach food items at or near the bottom
Probe	Inserting the bill into mud or matted vegetation to locate food items
Nibble vegetation	Nibbling the leaves, seeds, or inflourescenses of vegetation
Peck	Picking specific food items from the substrate
Snatch/snap	Snapping flying insects from the air
Manipulate food	Repositioning food item in bill before swallowing
Search	Locomotion and/or scanning movement interrupted only with foraging activities
Locomotion	
Fly	Flying not associated with courtship or agonistic activities
Swim	Swimming not associated with foraging or agonistic activities
Walk/run	Walking or running not associated with foraging or agonistic activities
Maintenance	
Bath	Wetting the feathers by head-dipping, wing-thrashing, somersaulting, or dashing-and-diving
Body-shake	Shaking the body to rearrange feathers or remove water from feathers; combined with swimming-body-shake; also includes infrequent shakes such as wing-shaking
Defecate	Voiding excrement
Drink	Dipping the bill into water and tipping the head back to swallow
Head-shake	Shaking the bill from side to side to remove water, feathers, or other particles from bill; includes head-flicks in which the head is jerked upward while shaken laterally and rotated around the anteroposterior axis
Preen	Oiling, cleaning, rearranging, and nibbling of feathers with bill or head; includes bill-cleaning during preening bouts
Scratch	Using the foot to scratch neck or head to relieve an irritation or remove feathers or particles

Appendix D. Continued.

Behavior	Description
Stretch	A variety of stretching movements including leg-stretch, wing-and-leg-stretch, both-wing-stretch, and jaw-stretch
Wing-flap	Fully opening and flapping wings to remove water, rearrange feathers, or perhaps increase bloody supply to flight muscles
Tail-wag	Shaking tail from side to side to remove water from tail or rearrange feathers

Rest

Rest	Includes resting, loafing, and sleeping; head and neck drawn in close to body or head tucked back behind wing
Brood	Female covering ducklings

Alert

Alert	Upright and erect posture with neck extended and motionless or scanning
Bill-flick	Rapid flicks of the bill associated with alert and agitated behavior
Flush	Sudden flight or escape as a result of disturbance
Head-pump	Bobbing the head up and down while alert or agitated; often precedes flight
Sky-look	Tilting the head laterally to view the sky
Submerged swim	Swimming with body fully or mostly submerged to escape disturbance
Vocalize	Calls associated with alert behavior and agitation

Courtship and display

Belly-preen	Similar to maintenance belly-preen, but performed by male in a more rigid manner and in a sideways orientation to the female
Body-shake	Similar to maintenance body-shake, but performed by male in a stiffer manner and in a sideways orientation to the female; includes swimming-body-shakes
Bridling	Male flings head upward and backward while extending upper body out of the water
Copulation	Male mounting female and copulating
Dash-and-dive	Rapid swimming, rushing, or shallow rising over the surface of water alternated with headlong diving into the water with wings partially opened or tucked back, in the context of courting
Down-up	Male tilts forward to submerge chest and dip bill into water and then jerks his head upward and vocalizes while holding his tilted position
Grunt-whistle	Male extends his upper body high out of the water while arching his bill downward across the water and to his chest and giving a nasal *raeb* call
Head-shake	Shaking of the head used in the preliminary stages of displaying; includes head-flicks

Appendix D. Continued.

Behavior	Description
Head-up-tail-up	Male abruptly jerks his head and tail feathers upward while pointing his bill towards female; frequently followed by nod-swimming
Inciting	Female follows mate while moving her bill back and downward to the side to incite male to respond with a display
Jump-flight	Steep 1-3 m ascent from water surface, followed by short (2-6 m), horizontal flight and steep splashing descent onto water
Leading	Male orientates the back of the head toward the female while swimming ahead of her
Nod-swim	Swimming low in water with neck out-stretched and occasionally nodding the head forward
Nuptial flight	One or more males pursuing a single female in swift, sometimes acrobatic flight; the female leads and may perform inciting displays
Pre-copulatory head-pump	Bobbing head up and down; generally more shallow, rapid, and rhythmic than typical 'alert' head-pump
Pre-copulatory prone position	Female partially submerged with flattened body and neck extended
Preen-behind-wing	Male moves bill over the inside of the wing feathers in a mock-preening motion; includes wing-flash display
Tail-wag	Wagging of the tail used in the preliminary stages of displaying
Turn-back-of-head	Male raises head and turns the back of the head towards the courted female
Wing-flap	Male flaps wings in a slower and more exaggerated manner than normal wing-flap

Intraspecific interactions

Aggression	Threats and aggressive behavior directed towards another Hawaiian Duck; these behaviors involve bill-flicking, bill-jabbing, bill-pointing, bill-threatening, chasing, feather-pulling, forced copulation, inciting, pecking, pursuit flights, vocalizing, and wing-flapping
Receive aggression	Receiving aggression from or submitting to another Hawaiian Duck
Gesture of repulsion	Female draws head back into shoulders, ruffles back and head feathers, fans tail, and opens bill widely while vocalizing
Mate-guard	Male maintains an alert posture and positions himself between his mate and other males and/or escorts other males away from mate

Interspecific interactions

Aggression	Threats and aggressive behavior directed towards another species
Receive aggression	Receiving aggression from or submitting to another species

Appendix D. Continued.

Behavior	Description
Pause	Recorded with behavior event (e.g., preening-pause is a brief pause between preening bouts)

Appendix E. Behavior and habitat use of Hawaiian Duck broods and brood-tending females at Hanalei National Wildlife Refuge on Kaua'i.

I recorded Hawaiian Duck (*Anas wyvilliana*) brood sightings at Hanalei National Wildlife Refuge (NWR), Kaua'i between September 2010 and August 2011 to assess seasonality of the annual cycle of Hawaiian Duck and to collect basic information on habitat use and behavioral patterns of broods. I estimated duckling age based on size and plumage class (Gollop and Marshall 1954) and recorded brood behavior at first detection. I classified Hawaiian Duck behaviors into six categories: foraging, resting and brooding, maintenance, locomotion, alert, and social. Habitat types were broadly classified as managed wetland and taro. Within taro, I categorized cover classes as taro, wet or dry non-vegetated fallow, wet or dry fallow with predominantly non-taro emergent vegetation, and harvested. Also, within the taro cover class, I categorized sub-classes based on taro cover: early growth (<25% cover), medium growth (25-50%), and dense growth (>50% cover). Within each habitat type, I recorded if individuals were in the unit or on a dike. I recorded if broods and brood-tending females were associated with males. Broods were differentiated based on chick age, location, and occasionally female characteristics. For each unique brood, I estimated hatch date based on age at first sighting, and I estimated incubation start date by assuming a 28-day incubation period (Swedberg 1967).

I used instantaneous focal sampling procedures (Altmann 1974) to quantify the diurnal time-activity budgets of Hawaiian Duck females with and without broods between September 2010 and August 2011. I recorded the behavioral activity of focal individuals at 10 sec sample intervals using a digital voice-activated recorder and electronic timer (Baldassarre et al. 1988, Dugger and Petrie 2000). Activity data were converted to proportions of time engaged in each behavior during each focal observation session (Baldassarre et al. 1988). Logit transformations were applied to proportions before analyses to improve homogeneity of variances and meet the assumption of normality (Ramsey and Schafer 2002). I used individual focal observation sessions as the sample unit to determine the relationship between dependent variables (proportion of time engaged in each behavioral state) and explanatory variables (e.g., breeding status). Factorial multivariate analysis of variance (MANOVA) using Wilks' lambda test

criterion was used to simultaneously evaluate the effects of explanatory variables on time-activity budgets (Ramsey and Schafer 2002). If MANOVA indicated significant effects of explanatory variables ($P < 0.05$), univariate analysis of variance (ANOVA) was used to examine the effects on separate behaviors after controlling for all other explanatory variables. If logit transformations failed to normalize the data and satisfy the equal variance assumption, I used the Kruskal-Wallis test to compare the untransformed proportion of time engaged in the activity between explanatory variables (Ramsey and Schafer 2002). I adjusted P-values using the Benjamini-Hochberg method to control the false discovery rate at 5% (Benjamini and Hochberg 1995). All time-activity budget values are reported as untransformed means ± standard error (SE).

RESULTS

Between September 2010 and August 2011, I recorded 178 Hawaiian Duck brood sightings, representing 67 unique broods, at Hanalei NWR. Most nests (70%) were initiated between December and May (exact binomial test; $P = 0.001$; Fig. E1). Broods were detected more frequently in taro (86%) than managed wetlands ($n = 174$; binomial test; $P < 0.001$; Table E1); however, detection rates of broods may vary between habitat types. Of broods sighted in taro, 31% were detected in the taro cover class and 53% on taro dikes. Within the taro cover class, most broods (91%) were observed in medium growth taro.

Across all habitat types, Hawaiian Duck broods ($n = 95$) were most frequently observed foraging (25%) and locomoting (43%) at first detection (Table E2). Broods in managed wetlands were observed foraging (27%) and locomoting (73%). Within taro, broods entered lo'i primarily to forage (50%), while broods used dikes for maintenance (31%), resting (21%), and locomotion (46%) activities.

Females with broods allocated activities differently than females without broods after accounting for time of day, month, and habitat type (MANOVA; Wilks' $\lambda = 0.88$, $F_{6,99} = 2.25$, $P = 0.044$; Table E3); however, the number of focal samples involving females with broods was limited ($n = 10$). Similar to Mottled Ducks (Paulus 1984), brood-rearing female Hawaiian Ducks exhibited more alert behavior than other females

using similar habitat types (21.2% vs. 6.7%). Male Hawaiian Ducks were associated with brood-tending females in 11.3% (19 of 168) of brood observations.

Although Hawaiian Duck broods were observed year-round, our results suggest that Hawaiian Ducks may exhibit subtle seasonality of the annual cycle with a peak in nesting activity between December and May. Brood observations also suggest that managed wetlands, as well as taro, are used by Hawaiian Ducks during brood rearing. Future studies involving radio-telemetry would provide a more complete picture of the timing of nesting and relative habitat use by Hawaiian Duck broods, which may help guide conservation and management actions (e.g., predator control efforts).

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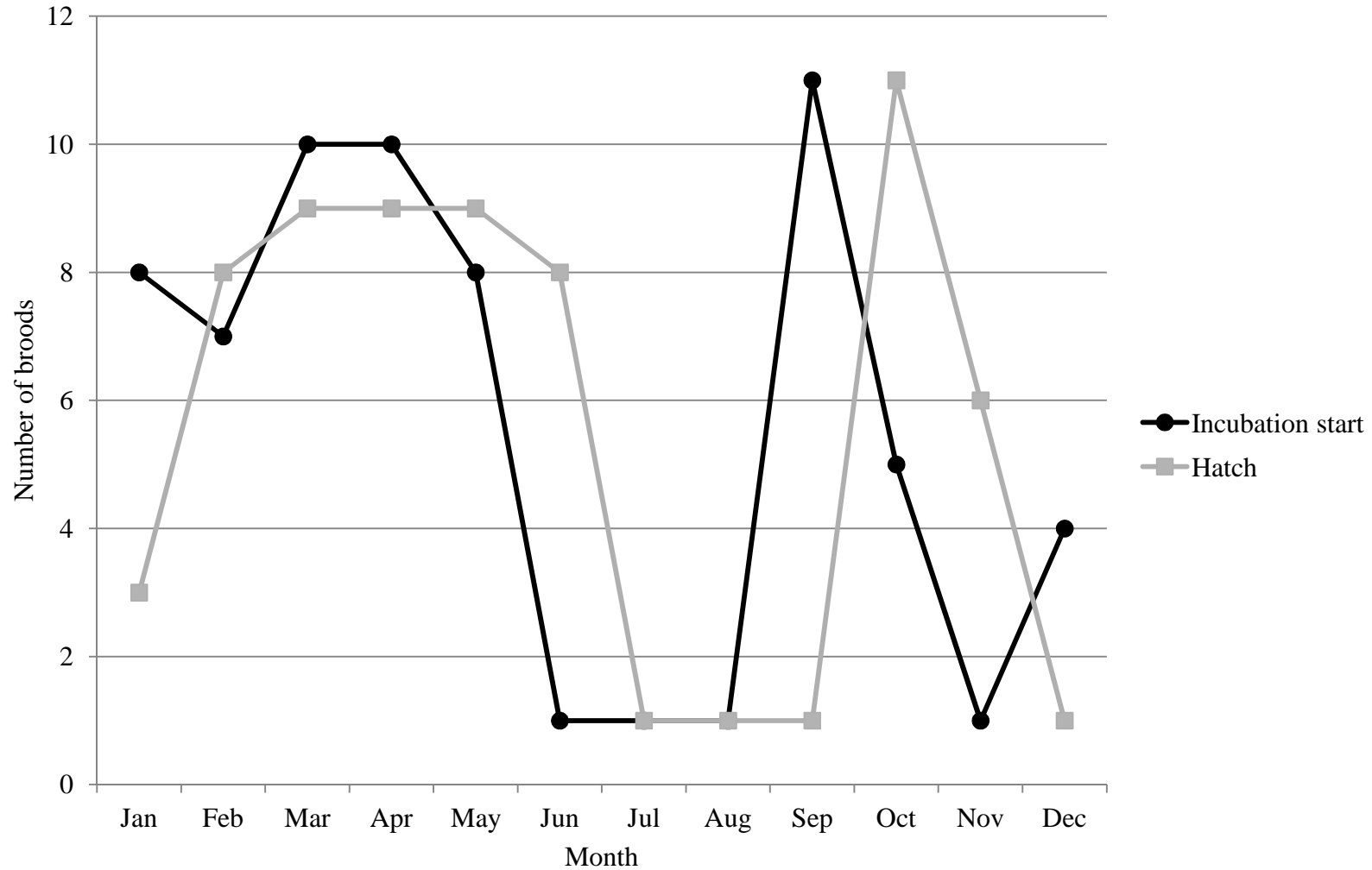
Figure E1. Monthly variation in the extrapolated incubation start dates and hatch dates of Hawaiian Duck nests based on broods observed at Hanalei National Wildlife Refuge, Kaua'i between September 2010 and August 2011 (n = 67 broods).

Table E1. Percentage of Hawaiian Duck broods ($n = 174$) observed in managed wetlands, taro loʻi, and ditches at Hanalei National Wildlife Refuge, Kauaʻi from September 2010 to August 2011.

Habitat type	Percentage of broods
Managed wetland	
Wetland	11.5
Dike	1.7
Taro	
Taro	26.4
Vegetated wet fallow	8.0
Non-vegetated wet fallow	4.0
Vegetated dry fallow	--
Non-vegetated dry fallow	1.1
Harvested	0.6
Dike	46.0
Ditch	0.6

Table E2. Activity budgets (%) of Hawaiian Duck broods using eight habitat types at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011 based on brood behavior at first detection ($n = 95$ observations).

| | | Percentage of broods engaged in each behavior | | | | | | | |
| | | Taro cover classes | | | | | | | |
Behavior	Managed wetland	Taro	Vegetated wet fallow	Non-vegetated wet fallow	Non-vegetated dry fallow	Harvested	Dike	Ditch	Overall
Forage	23.1	44.4	66.7	33.3	100.0	100.0	--	--	25.3
Maintenance	--	--	16.7	16.7	--	--	30.8	--	14.7
Rest and brood	--	7.4	--	--	--	--	20.5	--	10.5
Locomotion	76.9	37.0	--	50.0	--	--	46.2	--	43.2
Alert	--	11.1	16.7	--	--	--	--	100.0	5.3
Receive aggression	--	--	--	--	--	--	2.6	--	1.1
n	13	27	6	6	2	1	39	1	95

Table E3. Activity budgets ($\bar{x} \pm$ SE) of female Hawaiian Ducks with ($n = 10$ observation sessions) and without ($n = 110$) broods in taro loʻi at Hanalei National Wildlife Refuge, Kauaʻi from September 2010 to August 2011.

	Percent time spent per behavior		Test statistic value[a]	P-value
	With brood	Without brood		
Foraging	13.4 ± 9.5	21.1 ± 3.2	0.92 [KW]	0.338
Resting	38.4 ± 9.4	40.8 ± 3.6	0.04	0.842
Maintenance	22.0 ± 7.3	24.3 ± 2.7	0.12	0.727
Locomotion	4.8 ± 1.5	6.9 ± 0.9	0.20	0.656
Alert	21.2 ± 5.5	6.7 ± 0.7	7.99 [KW]	0.005
Social	0.2 ± 0.2	0.3 ± 0.1	< 0.01 [KW]	0.995

[a] Test statistics are F-values from separate ANOVAs unless otherwise indicated; [KW] Kruskal-Wallis H-values.

Appendix F. Relative frequency of occurrence (%) of foraging (*n* = 359 observation sessions; 42.9 hr), maintenance (*n* = 916; 79.3 hr), locomotor (*n* = 850; 39.3 hr), and social (*n* = 295; 2.6 hr) behaviors performed by Hawaiian Ducks in managed wetlands and cultivated taro lo'i at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011. Behaviors occurring less than 1.0% of the time are listed as trace (tr). Abbreviations for cover classes: VWF (vegetated wet fallow), NWF (non-vegetated wet fallow), VDF (vegetated dry fallow), NDF (non-vegetated dry fallow).

| Behavior | Managed wetlands | Taro lo'i | Taro lo'i cover classes | | | | | | | Overall |
			Taro	Harvest	VWF	NWF	VDF	NDF	Dike	
Forage										
Dabble	29.5	32.0	45.6	18.7	23.9	18.3	11.9	50.5	7.4	30.9
Head-dip	44.1	56.1	49.2	70.6	70.5	70.7	tr	--	--	51.0
Up-end	2.7	tr	--	tr	tr	1.2	--	--	--	1.3
Probe	13.9	3.8	1.3	3.5	tr	3.7	37.4	32.3	--	8.1
Nibble vegetation	4.3	1.4	tr	tr	1.6	tr	10.3	--	49.7	2.7
Peck	tr	1.0	tr	3.1	tr	tr	14.1	tr	tr	tr
Snatch/snap	tr	--	--	--	--	--	--	--	--	tr
Manipulate food	tr	tr	tr	tr	tr	tr	tr	2.2	1.1	tr
Search	3.9	4.5	2.5	2.7	3.1	5.0	20.5	14.3	41.1	4.2
Other	tr	tr	--	--	--	--	4.6	--	--	tr
n	208	151	62	14	15	34	4	2	20	359
Maintenance										
Preen	89.2	91.2	86.5	85.6	82.7	90.5	90.2	92.9	92.8	90.1
Bath	3.2	1.2	5.9	1.7	3.0	2.1	--	--	--	2.4
Scratch	1.9	1.9	1.7	1.7	3.6	1.9	--	2.7	1.9	1.9
Stretch	1.0	2.2	tr	1.7	1.5	tr	4.1	1.0	3.0	1.5
Tail-wag	1.4	1.3	1.4	2.9	1.6	2.0	2.1	1.4	1.1	1.4
Head-shake	tr	tr	tr	1.1	2.3	tr	2.1	tr	tr	tr

Appendix F. Continued.

Behavior	Managed wetlands	Taro loʻi	Taro loʻi cover classes							Overall
			Taro	Harvest	VWF	NWF	VDF	NDF	Dike	
Body-shake	tr	tr	tr	1.8	tr	tr	--	tr	tr	tr
Drink	tr	tr	1.2	1.9	3.6	1.1	1.5	tr	tr	tr
Wing-flap	tr	tr	1.3	1.5	1.4	tr	--	tr	tr	tr
Defecate	tr	tr	--	--	--	--	--	--	tr	tr
n	465	451	65	13	16	41	6	8	302	916
Locomotion										
Swim	87.9	44.1	81.4	88.2	82.6	74.3	--	--	tr	76.8
Walk/run	8.1	49.0	13.3	2.4	13.9	18.9	79.7	91.9	91.7	18.5
Fly	4.0	6.8	5.3	9.4	3.4	6.8	20.3	8.1	7.9	4.7
n	444	406	66	16	16	42	5	7	254	850
Social										
Courtship	39.3	17.0	37.8	50.0	62.4	--	--	--	1.1	33.0
Intraspecific agonistic	47.2	51.8	51.5	38.9	37.6	77.4	100.0	--	52.5	48.5
Interspecific agonistic	13.5	31.1	10.7	11.2	--	22.6	--	--	46.4	18.5
n	168	127	19	7	4	11	1	--	85	295

Appendix G. Mean proportion of time ($\bar{x} \pm$ SE) Hawaiian Ducks spent in agonistic interactions with other bird species ($n = 984$ observation sessions) and relative frequency (%) of interactions ($n = 131$) at Hanalei National Wildlife Refuge, Kaua'i between August 2010 and September 2011.

| Species | Aggression towards Hawaiian Duck | | Threats and aggression from Hawaiian Duck | |
	Percent of time	Relative frequency	Percent of time	Relative frequency
Hawaiian Moorhen	0.072 ± 0.010	44.4	0.008 ± 0.003	5.2
Hawaiian Coot	0.040 ± 0.009	24.7	0.001 ± 0.001	0.5
Hawaiian Stilt	0.023 ± 0.007	14.0	--	--
Hawaiian Goose	0.011 ± 0.004	6.6	0.001 ± 0.001	0.4
Other	0.001 ± 0.001	0.5	0.006 ± 0.003	3.9
Total	0.147 ± 0.015	90.1	0.016 ± 0.005	9.9

Appendix H. Waterbirds observed at Hanalei National Wildlife Refuge, Kauaʻi between August 2010 and September 2011. Symbols for status: Re (resident endemic species), Res (resident indigenous species; Hawaiian subspecies is endemic), Al (alien introduced species; long established and breeding since before 1945), An (alien introduced species; new introduction since 1945 and apparently established), Vc (visitor species; common migrant to Hawaii), Vr (visitor species; regular migrant to Hawaiʻi in small numbers in most or all years, Vo (visitor species; occasional migrant to Hawaiʻi in some to most years, Vs (visitor species; accidental straggler to Hawaiʻi); * listed as endangered on the Federal List of Endangered Species (Pyle 2002).

Family	Common name	Species	Status
Anatidae	American Wigeon	*Anas americana*	Vr
	Brant	*Branta bernicla*	Vo
	Bufflehead	*Bucephala albeola*	Vo
	Cackling Goose	*Branta hutchinsii*	Vr
	Gadwall	*Anas strepera*	Vs
	Green-winged Teal	*Anas crecca*	Vr
	Hawaiian Duck	*Anas wyvilliana*	Re*
	Hawaiian Goose	*Branta sandvicensis*	Re*
	Lesser Scaup	*Aythya affinis*	Vc
	Mallard	*Anas platyrhynchos*	Al, Vo
	Mallard-Hawaiian Duck hybrid	*Anas platyrhynchos x A. wyvilliana*	
	Muscovy	*Cairina moschata*	
	Northern Pintail	*Anas acuta*	Vc
	Northern Shoveler	*Anas clypeata*	Vc
	Ring-necked Duck	*Aythya collaris*	Vr
	Snow Goose	*Chen caerulescens*	Vs
Ardeidae	Black-crowned Night-heron	*Nycticorax nycticorax*	Ri
	Cattle Egret	*Bulbulcus ibis*	An
	Great Egret	*Ardea alba*	Vs
Charadriidae	Black-bellied Plover	*Pluvialis squatarola*	Vr
	Pacific golden Plover	*Pluvialis fluva*	Vc
Rallidae	Hawaiian Common Moorhen	*Gallinula choloropus sandvicensis*	Res*
	Hawaiian Coot	*Fulica alai*	Re*
Recurvirostridae	Hawaiian Black-necked Stilt	*Himantopus mexicanus knudseni*	Res*
Scolopacidae	Lesser Yellowlegs	*Tringa flavipes*	Vr
	Pectoral Sandpiper	*Calidris melanotos*	Vr
	Ruddy Turnstone	*Arenaria interpres*	Vc
	Sharp-tailed Sandpiper	*Calidris acuminata*	Vr
	Wandering Tattler	*Tringa incana*	Vc

Appendix H. Continued.

Family	Common name	Species	Status
Threskiornithidae	White-faced Ibis	*Plegadis chihi*	Vs

Appendix I. Comparison of time-activity budgets ($\bar{x} \pm$ SE) of Hawaiian Ducks in taro lo'i ($n = 163$ observation sessions) and on taro lo'i dikes ($n = 329$) at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011.

	Percent time spent per behavior			
Activity	In taro lo'i	On taro dike	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	361.68	< 0.001
Maintenance	21.6 ± 2.0	21.1 ± 1.2	0.29	0.591
Locomotion	12.7 ± 0.9	4.9 ± 0.4	81.52	< 0.001
Alert	7.5 ± 0.6	13.3 ± 0.8	15.32	< 0.001
Social	0.6 ± 0.1	0.4 ± 0.1	0.04 [KW]	0.836

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

Appendix J. Percentage of time spent foraging and resting ($\bar{x} \pm$ SE) by Hawaiian Ducks in six taro cover classes at Hanalei National Wildlife Refuge, Kaua'i from September 2010 to August 2011 (n = 163 observation sessions).

| Behavior | Taro | Harvested | Taro cover classes | | | |
			Vegetated wet fallow	Non-vegetated wet fallow	Vegetated dry fallow	Non-vegetated dry fallow
Forage	48.4 ± 3.9	62.8 ± 8.1	38.4 ± 7.4	40.5 ± 5.2	34.9 ± 13.6	22.6 ± 14.8
Rest	10.3 ± 2.3	6.4 ± 5.1	12.6 ± 6.2	9.0 ± 2.7	39.0 ± 18.1	47.9 ± 13.1
n	71	16	17	45	6	8

Appendix K. Percentage of Hawaiian Duck observation sessions with at least one anthropogenic disturbance within managed wetlands ($n = 492$) and taro loʻi ($n = 492$) at Hanalei National Wildlife Refuge, Kauaʻi between September 2010 and August 2011.
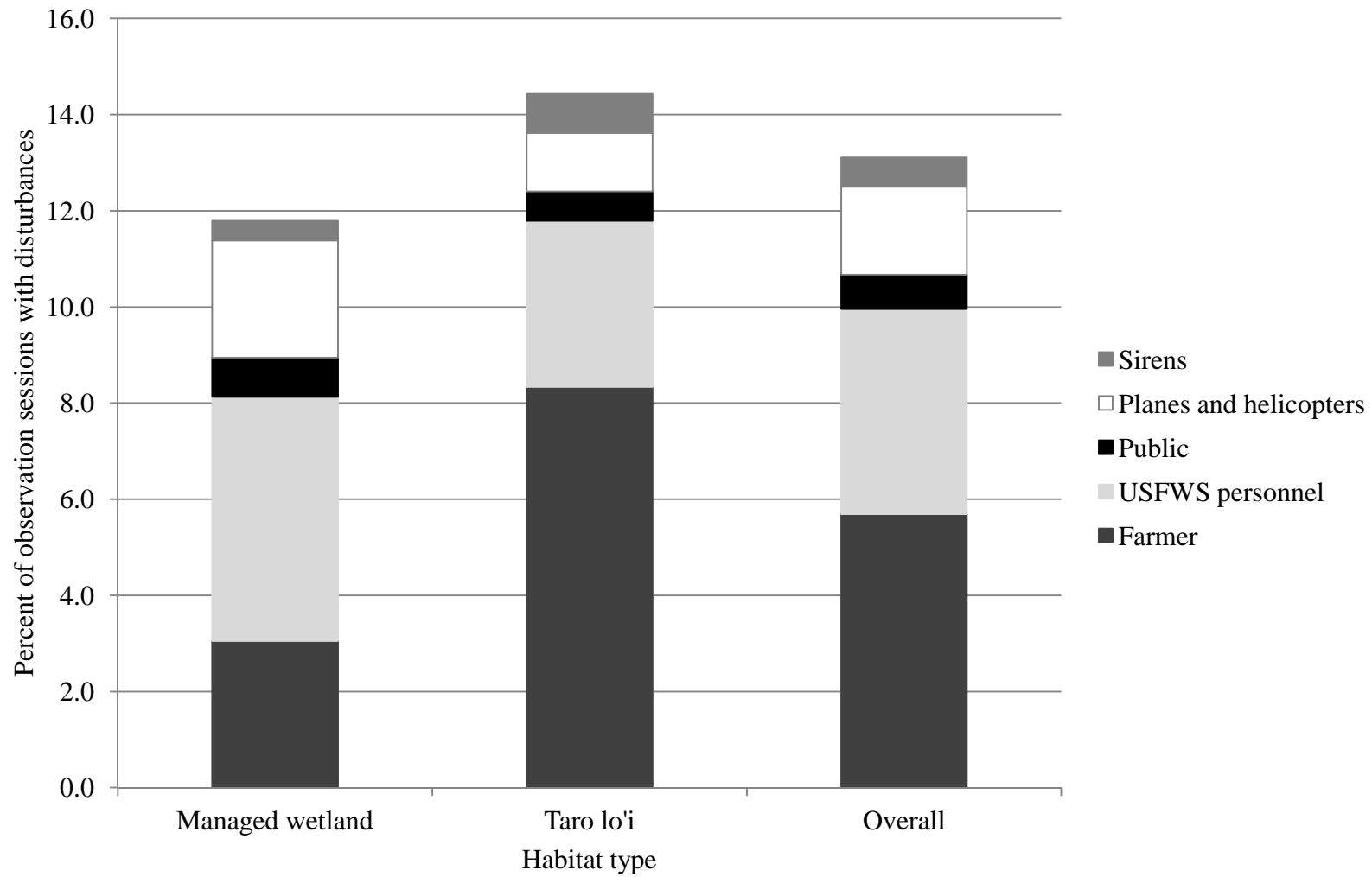
Appendix L. Relative frequency (%) of primary responses to anthropogenic disturbances at Hanalei National Wildlife Refuge, Kauaʻi between September 2010 and August 2011.

Disturbance type	n	Primary response		
		Alert	Take cover	Flush
Farmers	56	60.7	10.7	28.6
USFWS personnel	42	71.4	2.4	26.2
Public	7	57.1	28.6	14.3
Planes and helicopters	18	100.0	--	--
Sirens	6	100.0	--	--
Total disturbances	129	71.3	7.0	21.7

Appendix M. Monthly variation in the time-activity budgets of Hawaiian Ducks (*n* = 984 observation sessions) between September 2010 and August 2011 at Hanalei National Wildlife Refuge, Kaua'i.
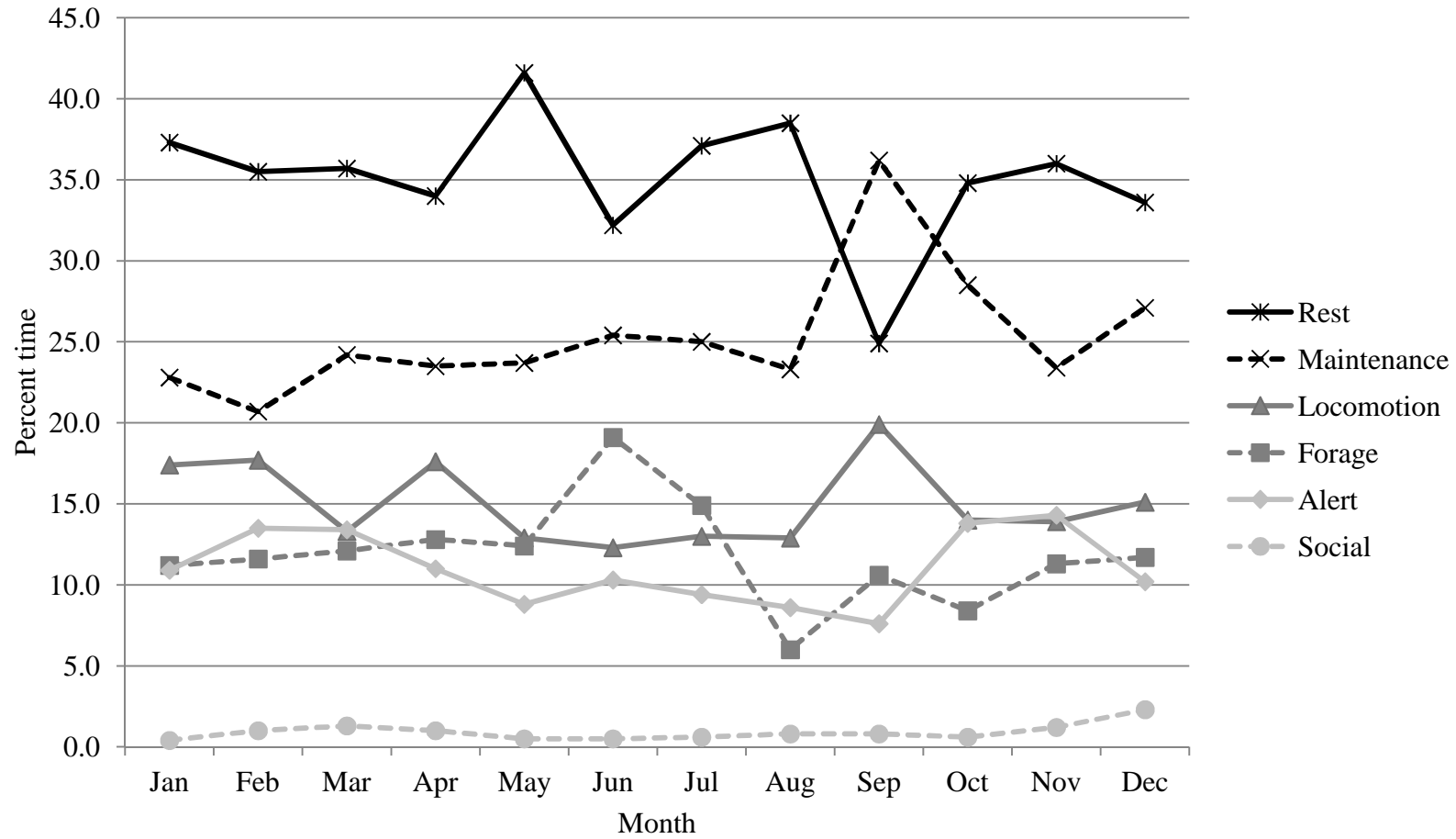
Appendix N. Monthly variation in percent time ($\bar{x} \pm$ SE) Hawaiian Ducks spent in agonistic interactions with other bird species at Hanalei National Wildlife Refuge, Kaua'i between September 2010 and August 2011 ($n = 984$ observation sessions).
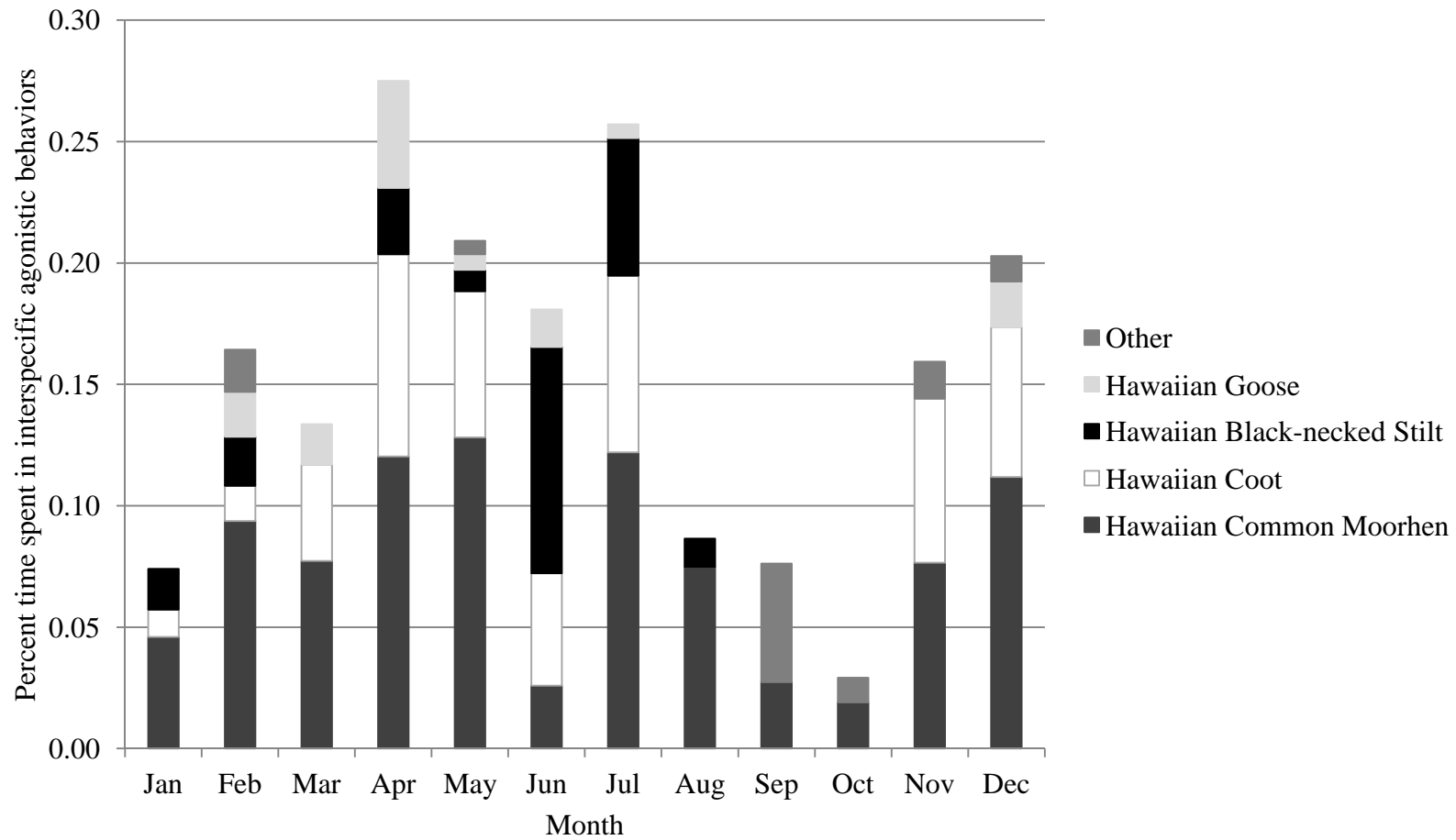
Appendix O. Diurnal variation in mean abundance of Hawaiian Ducks (birds/survey site; $\bar{x} \pm$ SE) using managed wetlands ($n = 751$ counts) and taro loʻi ($n = 580$) at Hanalei National Wildlife Refuge, Kauaʻi between September 2010 and August 2011.

| | n | Managed wetland | Taro loʻi | | | Overall |
			In loʻi	On dike	Taro total	
Early morning	367	2.7 ± 0.3	1.4 ± 0.2	1.3 ± 0.1	2.6 ± 0.3	2.7 ± 0.2
Late morning	335	1.6 ± 0.2	0.7 ± 0.1	1.3 ± 0.2	2.0 ± 0.2	1.8 ± 0.1
Afternoon	316	2.4 ± 0.3	0.8 ± 0.1	1.9 ± 0.2	2.7 ± 0.2	2.5 ± 0.2
Evening	313	4.3 ± 0.8	1.3 ± 0.2	1.8 ± 0.2	3.1 ± 0.3	3.8 ± 0.5
Overall	1,331	2.7 ± 0.2	1.0 ± 0.1	1.6 ± 0.1	2.6 ± 0.1	2.7 ± 0.1

Appendix P. Mean (± SE) water depth (cm), emergent wetland vegetation height (cm), total vegetative cover (%), and cover by *Cyperus* species (CYP; %), *Echininochloa crus-galli* (ECHCRU; %), *Fimbristylis littoralis* (FIMLIT; %), *Ludwigia octovalvis* (LUDOCT; %), *Paspalum urvillei* (PASURV; %), and *Urochloa mutica* (UROMUT; %) in eight managed wetland units at Hanalei National Wildlife Refuge, Kaua'i between September 2010 and August 2011.

Unit ID	Date	n	Depth	EVH	Total cover	CYP spp.	ECHCRU	FIMMIL	LUDOCT	PASURV	UROMUT
A1	09/22/10	30	7.1 ± 1.3	35.0 ± 4.8	56.7 ± 6.0	14.8 ± 4.2	4.9 ± 1.7	10.7 ± 2.7	9.6 ± 3.1	11.3 ± 3.9	4.4 ± 0.6
	10/27/10	30	8.6 ± 1.3	51.7 ± 6.9	68.5 ± 5.9	12.1 ± 3.2	9.1 ± 3.0	25.6 ± 6.6	8.2 ± 2.8	6.1 ± 3.4	6.1 ± 3.6
	12/24/10	30	6.5 ± 1.3	67.6 ± 6.9	73.8 ± 5.9	5.9 ± 1.2	18.3 ± 5.1	35.2 ± 7.0	12.4 ± 3.2	8.2 ± 3.6	4.5 ± 3.2
	02/26/11	30	2.1 ± 0.7	58.7 ± 6.2	65.9 ± 6.3	3.3 ± 0.7	7.9 ± 1.7	29.2 ± 5.9	12.4 ± 3.1	16.3 ± 4.3	5.0 ± 2.9
	04/16/11	30	6.9 ± 1.3	46.5 ± 5.1	66.3 ± 6.4	1.9 ± 0.7	6.9 ± 1.6	25.2 ± 5.9	10.4 ± 2.5	21.4 ± 5.3	2.3 ± 0.8
	06/27/11	30	11.3 ± 1.6	56.4 ± 6.6	61.3 ± 6.1	3.8 ± 1.3	4.5 ± 2.2	4.9 ± 1.5	11.3 ± 2.4	23.0 ± 5.1	4.6 ± 2.2
	08/13/11	30	10.5 ± 1.5	63.2 ± 7.9	61.6 ± 6.0	3.7 ± 1.0	2.8 ± 1.4	6.9 ± 2.4	13.7 ± 2.3	24.0 ± 4.9	7.0 ± 3.0
B3	09/28/10	30	5.7 ± 0.8	0.3 ± 0.2	0.4 ± 0.1	--	--	--	0.1 ± 0.1	--	--
	10/30/10	30	4.6 ± 0.7	3.7 ± 1.3	20.1 ± 6.4	--	0.3 ± 0.2	19.1 ± 6.2	1.3 ± 0.8	--	--
	12/26/10	30	0.8 ± 0.3	7.0 ± 2.3	24.6 ± 7.6	tr	0.6 ± 0.4	23.5 ± 7.4	0.8 ± 0.4	tr	tr
	02/25/11	30	1.4 ± 0.4	15.5 ± 3.0	50.7 ± 7.6	0.2 ± 0.1	1.9 ± 0.7	40.7 ± 7.0	9.2 ± 3.0	0.3 ± 0.3	0.1 ± 0.1
	04/17/11	30	--	23.1 ± 3.1	70.3 ± 6.8	0.5 ± 0.2	1.8 ± 0.8	65.3 ± 6.6	6.4 ± 2.2	2.5 ± 0.7	0.5 ± 0.3
	06/26/11	30	4.2 ± 0.7	27.7 ± 3.4	74.4 ± 6.2	2.4 ± 0.8	2.0 ± 0.8	61.2 ± 6.6	8.3 ± 2.9	6.3 ± 1.8	0.2 ± 0.2
	08/15/11	30	9.7 ± 0.9	23.3 ± 3.3	57.3 ± 6.0	4.0 ± 1.7	2.7 ± 0.5	41.5 ± 5.4	5.2 ± 1.4	5.6 ± 1.8	0.2 ± 0.2
B4	09/26/10	30	9.2 ± 1.2	28.8 ± 4.5	69.9 ± 5.4	7.4 ± 1.9	10.4 ± 4.6	47.3 ± 6.0	6.7 ± 2.4	2.7 ± 1.5	6.5 ± 4.5
	10/29/10	30	9.5 ± 1.2	31.6 ± 5.0	54.8 ± 6.5	8.8 ± 3.7	7.8 ± 3.5	31.5 ± 6.0	7.3 ± 2.3	6.8 ± 2.7	2.4 ± 1.6
	12/26/10	30	9.0 ± 1.4	29.7 ± 5.9	45.2 ± 6.8	2.8 ± 0.8	11.0 ± 4.5	18.3 ± 4.9	8.9 ± 2.3	5.8 ± 2.0	2.7 ± 1.9
	02/25/11	30	11.4 ± 1.3	28.4 ± 6.9	43.0 ± 6.7	1.2 ± 0.5	9.7 ± 4.7	10.4 ± 4.0	9.7 ± 1.9	9.7 ± 2.9	4.9 ± 3.0
	04/17/11	30	12.5 ± 1.4	22.9 ± 6.1	37.2 ± 6.2	1.3 ± 0.6	4.4 ± 2.6	9.5 ± 3.6	8.4 ± 1.6	11.5 ± 3.8	2.9 ± 1.9
	06/25/11	30	1.4 ± 0.6	35.8 ± 6.3	47.3 ± 6.8	6.2 ± 2.7	2.6 ± 1.6	6.8 ± 3.0	8.3 ± 2.0	17.0 ± 4.5	1.9 ± 1.1
	08/13/11	30	2.4 ± 0.7	55.5 ± 7.3	54.7 ± 6.5	5.4 ± 1.8	1.9 ± 1.0	13.4 ± 3.9	5.5 ± 1.3	15.7 ± 4.8	2.8 ± 1.5

Appendix P. Continued.

Unit ID	Date	n	Depth	EVH	Total cover	CYP spp.	ECHCRU	FIMMIL	LUDOCT	PASURV	UROMUT
C2	09/27/10	30	11.9 ± 1.4	67.2 ± 8.9	77.8 ± 5.7	6.0 ± 1.7	22.3 ± 5.9	37.4 ± 6.1	26.7 ± 4.4	0.2 ± 0.2	8.1 ± 4.0
	10/28/10	30	16.7 ± 1.3	57.7 ± 7.3	66.3 ± 5.8	4.6 ± 1.4	23.4 ± 5.7	26.1 ± 4.8	19.3 ± 3.2	0.2 ± 0.1	3.5 ± 2.0
	12/25/10	30	16.1 ± 1.4	46.5 ± 8.0	55.9 ± 6.2	3.7 ± 1.6	21.6 ± 4.9	11.9 ± 2.9	23.4 ± 3.4	--	4.2 ± 2.6
	02/23/11	30	6.0 ± 1.2	52.1 ± 7.4	54.7 ± 5.8	3.1 ± 1.0	13.4 ± 4.2	5.1 ± 2.1	30.0 ± 4.2	7.0 ± 2.9	9.5 ± 3.7
	04/16/11	30	15.5 ± 1.4	36.1 ± 5.3	42.6 ± 5.3	0.8 ± 0.5	1.5 ± 0.7	1.4 ± 1.3	26.7 ± 4.0	5.6 ± 2.1	5.3 ± 2.8
	06/26/11	30	6.2 ± 1.2	58.0 ± 7.3	46.8 ± 5.7	1.0 ± 0.4	3.0 ± 2.7	2.0 ± 1.6	26.2 ± 3.9	9.8 ± 3.3	4.9 ± 3.1
	08/15/11	30	5.6 ± 1.2	66.2 ± 7.8	47.7 ± 6.0	1.1 ± 0.5	3.6 ± 3.0	3.5 ± 2.4	23.7 ± 4.4	11.5 ± 3.9	4.5 ± 3.2
DU2	09/13/10	30	24.0 ± 2.7	47.4 ± 10.5	46.6 ± 8.3	0.3 ± 0.3	0.7 ± 0.7	0.3 ± 0.3	22.5 ± 6.1	--	27.0 ± 6.9
	10/26/10	30	30.8 ± 2.0	40.0 ± 9.0	39.5 ± 7.8	--	--	--	14.8 ± 4.2	--	25.8 ± 6.8
	12/22/10	30	14.7 ± 2.0	55.6 ± 10.8	37.6 ± 7.6	--	--	--	15.3 ± 4.7	--	21.0 ± 5.9
	02/27/11	30	18.7 ± 4.0	47.7 ± 10.8	38.0 ± 7.5	tr	--	--	10.9 ± 3.8	--	25.1 ± 6.4
	04/18/11	30	0.8 ± 0.4	62.1 ± 11.7	40.1 ± 7.5	--	--	--	9.3 ± 3.4	--	31.1 ± 7.1
	06/25/11	30	--	27.3 ± 5.6	64.0 ± 6.9	0.2 ± 0.1	5.1 ± 2.8	16.1 ± 4.9	12.5 ± 3.6	0.5 ± 0.5	33.9 ± 7.6
	08/12/11	30	9.7 ± 2.0	--	1.3 ± 0.7	--	--	tr	tr	--	1.2 ± 0.7
RM1	10/01/10	10	23.5 ± 3.9	--	7.4 ± 3.3	--	4.4 ± 2.6	--	2.0 ± 2.0	--	1.5 ± 1.2
	10/30/10	10	24.9 ± 4.2	2.1 ± 1.7	9.2 ± 3.6	--	4.1 ± 2.8	--	1.5 ± 0.9	--	0.6 ± 0.5
	12/22/10	10	25.2 ± 3.3	32.2 ± 14.0	25.3 ± 10.3	0.1 ± 0.1	21.8 ± 9.9	--	2.5 ± 1.4	--	4.0 ± 4.0
	02/24/11	10	15.6 ± 3.7	24.5 ± 9.7	19.5 ± 7.3	1.5 ± 0.8	3.5 ± 1.8	4.5 ± 4.5	4.6 ± 2.3	--	1.6 ± 1.3
	04/16/11	10	9.1 ± 2.6	35.0 ± 9.3	39.8 ± 10.3	3.4 ± 1.3	5.7 ± 2.9	13.8 ± 8.7	8.8 ± 3.8	--	1.1 ± 0.9
	06/27/11	10	7.7 ± 2.4	37.1 ± 10.2	39.1 ± 10.5	7.4 ± 3.9	3.4 ± 2.1	14.5 ± 8.9	6.5 ± 1.8	--	1.5 ± 0.8
	08/15/11	10	10.6 ± 2.7	36.8 ± 8.3	46.3 ± 12.5	3.2 ± 2.2	4.2 ± 1.9	15.7 ± 9.7	3.4 ± 1.3	--	2.6 ± 1.4
RM2	10/01/10	10	13.3 ± 2.4	0.6 ± 0.4	0.9 ± 0.5	--	--	--	0.2 ± 0.2	--	0.3 ± 0.3
	10/30/10	10	9.5 ± 1.6	2.9 ± 2.9	5.1 ± 4.5	--	--	--	0.1 ± 0.1	--	1.0 ± 0.7
	12/22/10	10	20.9 ± 3.0	30.1 ± 13.8	31.8 ± 10.3	0.8 ± 0.6	--	6.6 ± 3.9	5.0 ± 2.3	--	14.5 ± 7.8

Appendix P. Continued.

Unit ID	Date	n	Depth	EVH	Total cover	CYP spp.	ECHCRU	FIMMIL	LUDOCT	PASURV	UROMUT
	02/24/11	10	13.9 ± 2.9	18.5 ± 4.9	40.0 ± 8.2	1.8 ± 1.1	0.2 ± 0.2	28.0 ± 9.9	1.0 ± 0.5	--	6.7 ± 3.4
	04/16/11	10	--	36.3 ± 12.0	74.3 ± 9.4	4.7 ± 1.8	10.4 ± 8.9	36.2 ± 12.8	7.3 ± 2.4	--	5.4 ± 3.2
	06/27/11	10	6.4 ± 1.7	27.6 ± 5.5	75.5 ± 9.8	19.6 ± 7.4	2.5 ± 2.0	28.3 ± 9.1	7.8 ± 3.1	--	4.4 ± 2.6
	08/15/11	10	1.4 ± 1.0	26.6 ± 6.5	74.9 ± 9.7	17.3 ± 4.8	1.8 ± 1.2	38.0 ± 7.6	4.6 ± 2.0	--	3.3 ± 1.9
RM3	10/01/10	10	28.6 ± 3.6	0.6 ± 0.6	0.9 ± 0.8	--	--	--	--	--	0.1 ± 0.1
	10/30/10	10	35.4 ± 3.4	0.9 ± 0.9	0.5 ± 0.5	--	--	--	--	--	0.4 ± 0.4
	12/22/10	10	43.9 ± 2.3	8.5 ± 8.5	3.5 ± 3.5	--	--	--	--	--	3.5 ± 3.5
	02/24/11	10	5.1 ± 1.9	5.4 ± 1.9	20.8 ± 8.1	0.2 ± 0.2	--	15.7 ± 6.9	1.0 ± 0.6	--	0.8 ± 0.6
	04/16/11	10	--	21.5 ± 7.5	47.8 ± 15.2	2.6 ± 1.1	--	45.6 ± 15.2	3.5 ± 1.1	--	0.3 ± 0.3
	06/27/11	10	4.9 ± 1.7	30.6 ± 8.0	61.1 ± 14.4	3.2 ± 1.4	1.3 ± 0.7	56.3 ± 15.0	8.4 ± 3.9	--	--
	08/15/11	10	12.6 ± 2.0	23.8 ± 6.3	52.0 ± 12.6	1.9 ± 1.4	1.2 ± 0.9	42.1 ± 12.8	10.3 ± 6.3	--	0.3 ± 0.2

Appendix Q. Plant species occurring in wetlands at Hanalei National Wildlife Refuge, Kaua'i between September 2010 and August 2011. All species were detected in wetland sampling plots unless indicated by an asterisk (*). Status categories include indigenous (N) and introduced (I). Indicator status categories include obligate wetland (OBL; almost always is a hydrophyte, rarely in uplands), facultative wetland (FACW; usually is a hydrophyte but occasionally found in uplands), facultative (FAC; commonly occurs as either a hydrophyte or non-hydrophyte), and facultative upland (FACU; occasionally is a hydrophyte but usually occurs in uplands; Lichvar and Kartesz 2009).

Family	Scientific name	Common name	Status	Indicator status
Alismataceae	*Sagittaria latifolia*	arrowhead, swamp potato	I	OBL
Apiaceae	*Centella asiatica*	Asiatic pennywort	I	FAC
Araceae	*Colocasia esculenta* *	kalo, taro	I	OBL
Asteraceae	*Ageratum houstonianum*	bluemink	I	FACU
	Eclipta prostrate	false daisy	I	FACW
	Emilia fosbergii	pualele	I	FACU
	Sphagneticola trilobata	wedelia	I	FAC
Azollaceae	*Azolla filiculoides* *	large mosquito fern	I	OBL
Caryophyllaceae	*Drymaria cordata* var. *pacifica*	pipili, whitesnow	I	FAC
Commelinaceae	*Commelina diffusa*	honohono, climbing dayflower	I	FACW
Convolvulaceae	*Ipomoea triloba*	littlebell	I	FAC
Cyperaceae	*Cyperus difformis*	variable flat sedge	I	OBL
	Cyperus javanicus	Javanese flat sedge	N	FACW
	Cyperus odoratus	rusty flat sedge	N	FACW
	Cyperus pilosus	fuzzy flat sedge	I	FACW
	Cyperus polystachyos	many-spike flat sedge	N	FACW
	Fimbristylis dichotoma	forked fimbry	N	FAC
	Fimbristylis littoralis	grass-like fimbry	I	OBL
	Kyllinga brevifolia	short-leaf spike sedge	I	FAC
	Schoenoplectus juncoides	rock bulrush	N	OBL

Appendix Q. Continued.

Family	Scientific name	Common name	Status	Indicator status
Euphorbiaceae	*Phyllanthus debilis*	Niruri	I	FAC
Fabaceae	*Desmodium triflorum*	three-flower tick-trefoil	I	FAC
	Macroptilium lathyroides	wild bushbean	I	FACU
	Mimosa pudica var. *unijuga*	sleeping grass	I	FACU
Lemnaceae	*Lemna aequinoctialis* *	Lesser duckweed	I?	OBL
	Wolffia globosa *	Asian watermeal	I	OBL
Lythraceae	*Ammannia coccinea*	valley redstem	I	OBL
Lythraceae	*Cuphea carthagenensis*	Colombian waxweed, tarweed	I	FAC
Myrsinaceae	*Ardisia elliptica*	shoebutton ardisia	I	FACU
Onagraceae	*Ludwigia octovalvis*	Mexican primrose-willow	I?	OBL
	Ludwigia palustris	marsh purslane	I	OBL
Poaceae	*Andropogon bicornis*			
	Chloris radiata *	radiate fingergrass	I	FACU
	Coix lachryma-jobi	Job's-tears	I	FACW
	Echinochloa crus-galli	barnyard grass	I	FACW
	Panicum maximum	Guinea grass	I	FACU
	Paspalum conjugatum	Hilo grass	I	FAC
	Paspalum fimbriatum	Panama crown grass	I	FAC
	Paspalum scrobiculatum	ditch millet, Indian crown grass	N?	FAC
	Paspalum urvillei	Vasey's grass	I	FAC
	Paspalum vaginatum	saltwater couch, seashore paspalum	I	FACW
	Sacciolepis indica	glenwood grass	I	FAC
	Setaria spp.		I	
	Urochloa mutica	California grass	I	FACW

Appendix Q. Continued.

Family	Scientific name	Common name	Status	Indicator status
Pteridaceae	*Ceratopteris thalictroides*	watersprite	I	OBL
Rubiaceae	*Spermacoce assurgens*	woodland false buttonweed	I	FAC