Articles

Estimation of Vital Rates for the Hawaiian Gallinule, a Cryptic, Endangered Waterbird

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Abstract

Vital rates describe the demographic traits of organisms and are an essential resource for wildlife managers to assess local resource conditions and to set objectives for and evaluate management actions. Endangered waterbirds on the Hawaiian Islands have been managed intensively at state and federal refuges since the 1970s, but with little quantitative research on their life history. Information on the vital rates of these taxa is needed to assess the efficacy of different management strategies and to target parts of the life cycle that may be limiting their recovery. Here, we present the most comprehensive data to date on the vital rates (reproduction and survival) of the Hawaiian gallinule *Gallinula galeata sandvicensis*, a behaviorally cryptic, endangered subspecies of wetland bird endemic to the Hawaiian Islands.
Islands that is now found only on Kaua‘i and O‘ahu. We review unpublished reproduction data for 252 nests observed between 1979 and 2014 and assess a database of 1,620 sightings of 423 individually color-banded birds between 2004 and 2017. From the resighting data, we estimated annual apparent survival at two managed wetlands on O‘ahu using Cormack–Jolly–Seber models in program MARK. We found that Hawaiian gallinules have smaller mean clutch sizes than do other species in the genus Gallinula and that clutch sizes on Kaua‘i are larger than those on O‘ahu. The longest-lived bird in our dataset was recovered dead at age 7 y and 8 mo, and the youngest confirmed age at first breeding was 1 y and 11 mo. In 4 y of monitoring 14 wetland sites, we confirmed three interwetland movements on O‘ahu. In our pooled dataset, we found no statistically significant differences between managed and unmanaged wetlands in clutch size or reproductive success, but we acknowledge that there were limited data from unmanaged wetlands. Our best supported survival models estimated an overall annual apparent survival of 0.663 (95% CI = 0.572–0.759); detection varied across wetlands and study years. First-year survival is a key missing component in our understanding of the demography of Hawaiian gallinules. These data provide the foundation for quantitative management and assessment of extinction risk of this endangered subspecies.

Keywords: *Gallinula galeata sandvicensis*; island bird; moorhen; population viability; program MARK; reproductive success; survival rate

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**Introduction**

Vital rates, which include reproduction and survival rates, are the basic components of life tables and population models (Caughley 1977; Morris and Doak 2002). Quantifying vital rates is a priority for increasing the efficacy of species conservation and management (Tuljapurkar and Caswell 1997; Taylor et al. 2012). Specifically, vital rates are central to endangered species recovery planning because they are used for population viability analysis (Beissinger and Westphal 1998; Reed et al. 2002), they guide harvest rate assessments for sustainable resource management (Taylor et al. 1987), and vital rate sensitivity analysis is used to guide some management activities (Wisdom et al. 2000; Açıçakaya et al. 2003; Reed et al. 2009). Reduction in vital rates can contribute to critical slowing down, which is an increase in recovery time to equilibrium after perturbation for populations in some nonlinear systems that are near a tipping point (Wissel 1984; Ghandi et al. 1998; also referred to as resilience, Holling 1973). It has been suggested that population growth rate, particularly within the context of recovery after a perturbation, might be an excellent metric for evaluating population health and might act as an early warning signal of impending collapse (Wissel 1984; Sibly and Hone 2002; van Nes and Scheffer 2007). Vital rates are also commonly used as indices of habitat quality (e.g., Todd and Rothermel 2006), particularly where the abundance of a species might otherwise be misleading (e.g., Hagan et al. 1996; Purcell and Verner 1998), but this should be done with caution because values for a population near carrying capacity that exhibits density-dependent growth might be difficult to interpret (Watkinson and Sutherland 1995). As such, vital rates are a major resource for a wildlife manager’s toolbox by acting as a barometer for a population’s overall condition and enabling quantitative analysis for evidence-based conservation and management.

The Hawaiian gallinule *Gallinula galeata sandvicensis*, an endangered subspecies of the common gallinule (Figure 1), is currently endemic to shallow, coastal freshwater wetlands on O‘ahu and Kaua‘i (Hawai‘i, USA). Hawaiian gallinules were reported as being common on all of the five main Hawaiian Islands during the 1890s (reviewed by Shallenberger 1977; Banko 1987), but they began exhibiting dramatic population declines and range retractions during the early 20th century. By 1947, the species was reported as extirpated from the island of Hawai‘i and as “precarious” on Maui, Moloka‘i, and O‘ahu (Schwartz and Schwartz 1949; Shallenberger 1977). Declines were driven by habitat loss and predation by introduced mammals (Griffin et al. 1989; Chang 1990). Hawaiian gallinules reached their lowest numbers in the
C.B. van Rees et al.

Figure 1. In this study, we collected all available information on the vital rates of the Hawaiian gallinule Gallinula galeata sandwicensis on Oʻahu and Kauaʻi by using mark–resight and nest monitoring data from 1979 to 2017. These images depict an adult Hawaiian gallinule and gallinule nest at Olomana golf links, Kailua, Oʻahu, Hawaiʻi. Photos taken in 2016 by A. Sandor.

Early 1960s, with an estimated 57 individuals (Engilis and Pratt 1993), although visual survey methods are recognized as being underestimates because of the species’ secretive nature, and early surveys did not incorporate their entire possible range (Shallenberger 1977; DesRochers et al. 2008). With legal protection as endangered (U.S. Department of the Interior 1967) under the U.S. Endangered Species Act (ESA 1973, as amended) and active habitat and predator management, Hawaiian gallinules have since increased to an estimated 600 individuals, but the subspecies is still limited to two islands (Reed et al. 2011).

Hawaiian gallinules are considered to be conservation reliant because their wetland habitats require continual management to exclude exotic, invasive plants and predators (Reed et al. 2012; Underwood et al. 2013). In addition to constant vegetation management, trapping predators (e.g., small Indian mongoose Herpestes javanicus) and careful management of water levels to prevent flooding and create breeding and feeding habitat are common activities in Hawaiian waterbird conservation (VanderWerf 2012). Although Hawaiian gallinules persist in small numbers in relict and artificial wetland habitats (e.g., golf course water hazards, lotus Nelumbo nucifera farms, water features in gardens) on both islands, managed and protected wetlands at James Campbell National Wildlife Refuge (JCNWR) and Hamakua Marsh on Oʻahu and Hanalei National Wildlife Refuge on Kauaʻi are current strongholds for the subspecies (U.S. Fish and Wildlife Service [USFWS] 2011). Threats to the subspecies are similar on the two islands, but with some notable differences (Reed et al. 2012). For example, gallinule populations on both islands are threatened by introduced predators and wetland loss. However, wetland loss has been substantially higher on Oʻahu (≥65%) compared with loss on Kauaʻi (8%; van Rees and Reed 2014), and the introduced small Indian mongoose is numerous on Oʻahu, but not established on Kauaʻi (Hays and Conant 2007; USFWS 2011). Avian botulism caused by Clostridium botulinum is an additional risk factor for Hawaiian waterbirds (Brock and Breese 1953; Morin 1996; Work et al. 2010) and is more common on Kauaʻi than on Oʻahu (K.U. and J.G.U., personal observations). However, any significant effect on the vital rates of Hawaiian gallinules is unknown, and baseline information on vital rates is necessary to understand the impacts of this and other potential threats to the subspecies.

Despite being federally protected, with substantial resources allocated to studying their ecology, status, and management (DesRochers et al. 2009, 2010; Gutscher-Chutz 2011; Reed et al. 2011, 2012; USFWS 2011; Underwood et al. 2013), published data on vital rates for this subspecies are limited or absent. A single published paper (Byrd and Zeillemaker 1981) and three unpublished theses (Nagata 1983; Chang 1990; Gee 2007) are the only reports of Hawaiian gallinule reproduction, and to date there have been no studies of survival rates. This is likely due, in part, to the cryptic behavior of the subspecies. Species-specific call–response surveys are required to effectively detect Hawaiian gallinules in the field, where birds are often concealed from view by dense vegetation (DesRochers et al. 2008). Furthermore, visual observations of nests and young are difficult because they are obstructed by dense emergent vegetation (Byrd and Zeillemaker 1981; Gee 2007). Estimation of vital rates is an important part of long-term conservation planning for Hawaiian gallinules, which calls for quantification of extinction risk through population viability analysis (Mitchell et al. 2005; USFWS 2011; VanderWerf 2012). Vital rate estimates are also important for improving recovery plans for this subspecies and will allow for comparisons among islands and sites to ascertain under what conditions gallinules do best and also to distinguish source and sink populations (e.g., Dias 1996). Until recently, nothing was known about the movement behavior and population structure of Hawaiian gallinules in their apparently relict, fragmented wetland habitats, but recent work by van Rees et al. (2018) showed evidence of low geneflow between many wetlands on Oʻahu, indicating that movement rates may currently be very limited on that island. Field study on the movement rates of this taxon is also needed to inform its management and conservation.

Our objectives were to 1) summarize unpublished data on reproduction (clutch size, hatching rate, nest fate,
methods

reproduction

All known, unpublished data on reproduction for the Hawaiian gallinules were collected from studies conducted from 1979 to the present on the islands of Kaua‘i (22.065143°N, −159.517492°W) and O‘ahu (21.455580°N, −158.038709°W) in Hawai‘i, USA. We were unable to obtain the raw data from the single published study (Byrd and Zeillemaker 1981) after contacting the authors, so we compare our results with theirs. Due to the potential for differences among nest-monitoring protocols between the studies included in our synthesis, we analyzed data first by study and then for all studies as a meta-analysis. Because a larger, synthesized (although possibly less precise) dataset might be useful to managers in certain contexts (e.g., population viability analysis, Morris and Doak 2002), we also pooled the raw data from these studies and conducted overall comparisons between islands and management and nonmanagement settings. This pooled dataset excludes data for reproductive vital rates for which monitoring methods indicated that they might yield biased estimates (see below and Supplemental Material). For the pooled dataset, we compared reproduction metrics of Hawaiian gallinules between managed and unmanaged habitats, between islands (O‘ahu vs. Kaua‘i), and with conspecific data.

Reproductive data documented in this study included clutch size, brood size, and nest fate. For nest success in both our pooled dataset and meta-analysis, we excluded observations from which nest fate could not be unambiguously confirmed (e.g., chicks sighted nearby after termination of nesting activity, but unclear whether those chicks indeed hatched from that nest) and if insufficient or inconsistent information in raw data gave ambiguity to the observations at a single nest. Thus, our summary statistics may differ from those presented in the written accounts of some of these studies (e.g., the three Master’s theses Nagata [1983]; Chang [1990]; Gee [2007]).

All studies of reproductive success used behavioral observations taken during prolonged periods in the field to locate nests and defined a nest as successful if at least one egg hatched. All researchers noted when egg counts may not have been completed clutches (due to premature failure, or discovery of the nest late in the nesting cycle). Where possible, all researchers associated broods with nests based on visual inspection of the nest (evidence of hatching, no evidence of nest depredation), or chick activity around nest. We excluded all data that had no confirmation of nest success, hatch rate, or clutch completion when calculating relevant vital rates. Nagata (1983) and J.L.G.-C. (this study) encountered nests incidentally to other work in wetland habitats, so their sampling was haphazard. Once found, Nagata (1983) monitored nests through weekly visits, whereas J.L.G.-C. only recorded data from incidental nest encounters. Chang (1990) located nests by using exhaustive surveys (walking through the entirety of a pond and searching emergent vegetation) of study sites every 2–3 wk and visited nests twice per week once they had been located to monitor clutch completion. Chang (1990) also monitored broods twice weekly for 30-min periods. Gee (2007) also used exhaustive surveys to locate nests and playback surveys to locate nesting birds. He marked individual eggs to monitor egg loss throughout the nesting cycle and visited nests three times per week until clutch completion was evident, and he monitored broods during weekly waterbird surveys of study sites. J.C. and M.S. (this study) visited nests once per week from nest discovery to hatching. Posthatch, all researchers except J.L.G.-C. (this study) checked nests for signs of unhatched eggs. Because J.L.G.-C.’s data did not involve repeated visits to nests to confirm clutch size or posthatch brood size, they were excluded from our pooled dataset. All other studies were retained in the analysis, because their methods were deemed sufficiently similar to have not strongly bias separate estimates. We also opportunistically collected data for additional vital rates that are necessary for population viability analysis, but for which only limited or anecdotal accounts are available, and synthesized these data for publication. In particular, we sought information on the prevalence and degree of multiple brooding (i.e., successfully breeding multiple times per year), the maximum number of broods produced in a year, and evidence of reproductive senescence.

survival and movement

Survival estimates were derived from recaptures and sightings (including banding as the first encounter) of uniquely marked (color-banded) gallinules on O‘ahu. Banding of Hawaiian gallinules on O‘ahu started in 1979 at private lotus farms and the Hamakua Marsh wildlife sanctuaries (Dibben-Young 2010). Extensive marking and resighting efforts on Hawaiian gallinules did not begin until 2004 (Dibben-Young 2010) and occurred on an irregular, ad hoc basis for the next decade, primarily at JCNWR (O‘ahu), where the most banding occurred. Starting in 2014, annual surveys from May to August were conducted island-wide, and we expanded banding
efforts to include wetlands across the entire island of O'ahu (Figure 2). May–August survey periods were chosen due to the availability of personnel, but they are not considered a source of bias given the absence of a strong annual cycle in Hawaiian gallinule life history (DesRochers et al. 2009; USFWS 2011). Birds were identified by a unique combination of colored plastic (Darvic) leg bands and an aluminum U.S. Geological Survey leg band. Resightings were acquired during biannual surveys and recapture and recovery, our ongoing citizen-science monitoring program started in 2014 (http://sites.tufts.edu/Hawaiianmoorhen), and as ad hoc observations. For ambiguous resightings (partial combinations seen) or birds with missing color bands, we checked all possible bird identities for a given resighting; if only one individual was possible (i.e., other candidates seen elsewhere at the same time, or known dead), we recorded the sighting as that individual. If no single possible candidate was available, we excluded the record. Hawaiian gallinules cannot be sexed visually in the field (Bannor and Kiviat 2002), so we were unable to analyze data separately by sex. We used this database to estimate mean annual apparent survival of adults, and we reviewed written, unpublished reports from the surveyed studies to find accounts of posthatching and postfledging (chick and juvenile) survival. We were unable to conduct mark–resight studies on chicks because they could not be safely banded at that stage. We also used our resighting database to document movements between islands and between wetland habitats on O'ahu.

We estimated yearly apparent survival (the estimated survival parameter used in mark–recapture frameworks, wherein mortality is indistinguishable from repeated failure of detection or permanent emigration) by using standard Cormack–Jolly–Seber (CJS) models in programs MARK 8.2 (White and Burnham 1999) and R (R Core Team 2015). Years were determined based on calendar date (years start January 1 and end December 31), which was chosen for computational convenience. As with banding field seasons, the year was not considered to be a source of bias because of the weak seasonal breeding phenology of Hawaiian gallinules (DesRochers et al. 2009; USFWS 2011) and because the majority (>70%) of marking and sighting events occurred during May–August. Resighting data were converted to yearly encounter histories and MARK input files by using an R script written by the authors. To prevent violation of the CJS model assumption of relatively small survey periods compared with between-encounter intervals, we restricted our analysis to resightings in May and June, when most sightings occurred. We compared the likelihood of a suite of potential survival models in MARK by using Akaike’s Information Criterion corrected for small sample size (AICc) (Sugiura 1978; Hurvich and Tsai 1989; Burnham and Anderson 1998). These were a null model (constant \( \phi \) [survival] and \( p \) [detection]); a time model for detection (constant \( \phi \), and \( p \) varies by study year); a
wetland model for survival ($\phi$ varies by wetland, constant $p$); a time model for survival and detection ($\phi$ and $p$ vary by study year); three by-wetland survival models ($\phi$ varies by wetland, and $p$ is either constant, varies by study year, or varies by wetland); and four models where $p$ varied by wetland, year, and their interaction ($\phi$ was either constant, or varied by year, wetland, or their interaction).

We implemented four tests of goodness of fit (TEST.SR, TEST.SM, TEST.CT, TEST.CL) in program U-CARE (Choquet et al. 2009) to evaluate the fit of a CJS model with and without wetland groupings. We also evaluated goodness of fit of our general model ($\phi$ and $p$ vary by wetland, year, and their interaction) by using the bootstrapping goodness-of-fit test in MARK. Following Couch and White (2015), we checked for overdispersion by comparing the observed deviance of the full model to the range of deviances from 1,000 bootstrap simulations of the model and calculated a $p$-value based on the rank of the observed deviance. We also estimated $\hat{c}$ (a measure of overdispersion) by dividing the observed deviance by the average deviance of 1,000 bootstrap simulations. Because this process showed interspersion and some lack of fit for our full dataset when observations from all sampled wetlands were included, we reduced our dataset to the two wetland sites with the most extensive histories of mark–resights (JCNWR and Waimea Valley) and carried out all analyses with birds from these wetlands only. We observed no evidence of overdispersion or poor model fit by using this reduced dataset. We also examined individual life histories to find the oldest Hawaiian gallinules among all banded birds.

**Results**

**Reproduction**

Our data on reproduction came from 252 individual nests monitored on Kaua‘i and O‘ahu from 1979 to 2014. Reproductive data were collected at eight different locations, including National Wildlife Refuges with active predator control and wetland management (Table 1). All studies except for Gutscher-Chutz (2011) and Gee (2007) had lower clutch sizes, and all except for Chang (1990) had lower nest success, than those reported by Byrd and Zeillemaker (1981) (mean nest success = 0.75, mean clutch size = 5.6) from 64 clutches on the same island from 1975 to 1980 (Table 2). Gee (2007), Gutscher-Chutz (2011) data, and Chang (1990) had higher mean numbers of chicks per successful nest than Byrd and Zeillemaker (1981). Notably, hatch rates (the proportion of eggs per nest that hatched) were much smaller than those reported by Byrd and Zeillemaker (1981); in the case of our meta-analysis average, they were 50% smaller. Data from J.L.G.-C. (this study) showed extremely low nest success, number of chicks per nest, and overall hatch rate, but a high number of chicks per successful nest. Generally, studies from O‘ahu (Chang, 1990; Silbernagle, unpubl. data Nagata, 1983) showed somewhat smaller clutch sizes than those on Kaua‘i (H.K.W.G., J.L.G.-C., and J.C.). M.S. (this study) and Chang (1990), working on wildlife refuges on O‘ahu, saw higher hatch rates than any of the studies on Kaua‘i.

Our pooled dataset included clutch size data from 125 nests on Kaua‘i and 127 nests on O‘ahu (Table S1, Supplemental Material). Pooled clutch sizes on Kaua‘i were very similar those of Byrd and Zeillemaker (1981). Nest success, number of chicks per successful nest, and hatch rate, in contrast, were all lower for our pooled dataset than the values reported by Byrd and Zeillemaker (1981), and hatch rates for Kaua‘i were much lower. Hawaiian gallinule clutch sizes in this study ranged from 2 to 11 eggs (Table S1, Supplemental Material). Comparing between islands in our pooled dataset, nests on Kaua‘i had significantly larger clutch sizes than did nests on O‘ahu (Welch’s $t$-test, $t = 4.40, df = 169.68, P < 0.001$), although nest success (the proportion of nests that hatched at least one chick) did not differ significantly between the islands (Welch’s $t$-test, $t = -0.46, df = 212.09, P = 0.65$; Table S1, Supplemental Material). Clutch sizes on O‘ahu ranged from 2 to 8 eggs, whereas those on Kaua‘i ranged from 2 to 11. Nests on O‘ahu produced a similar number of chicks per nest (Welch’s 2-sample $t$-test, $t = -1.73, df = 219.99, P = 0.08$) but a higher number of chicks per successful nest (Welch’s 2-sample $t$-test, $t = -2.64, df = 135.19, P < 0.01$; Table S1, Supplemental Material). Using our pooled dataset, we saw no

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**Table 1.** We collected unpublished studies on Hawaiian gallinule *Gallinula galeata sandvicensis* reproductive vital rates from studies conducted on Kaua‘i and O‘ahu from 1979 to 2014. This table shows the study type, location, and years of data collection for each of these studies and whether study sites were managed or unmanaged. All Master’s theses are listed with their date of completion and can be found in the references of this paper; their vital rates data have not been previously published in the peer-reviewed literature. The data of Nagata (1983) at several lotus farms is the only reproductive data from unmanaged wetlands used in this study.\(^a\)

| Study                    | Study type        | Island (location)                  | Managed? | Years of data collection |
|--------------------------|-------------------|------------------------------------|----------|--------------------------|
| Nagata (1983)            | Master’s thesis   | O‘ahu (Hamakua and lotus farms)    | Yes/No   | 1979–1980                |
| Chang (1990)             | Master’s thesis   | O‘ahu (JCNWR, Pearl Harbor NWR)    | Yes      | 1985–1988                |
| Gee (2007)               | Master’s thesis   | Kaua‘i (Hanalei NWR, Adjacent Taro fields) | Yes      | 2004                     |
| Silbernagle (USFWS)      | Unpublished data study | O‘ahu (JCNWR, Pearl Harbor NWR)    | Yes      | 1997–2001, 2004, 2006    |
| Gutscher-Chutz (2011)    | Unpublished data study | Kaua‘i (Hanalei NWR)               | Yes      | 2005                     |
| Cosgrove (USFWS)         | Unpublished data study | Kaua‘i (Hanalei NWR)               | Yes      | 2014                     |

\(^a\) JCNWR = James Campbell National Wildlife Refuge; NWR = National Wildlife Refuge; USFWS = U.S. Fish and Wildlife Service.
Table 2. We reviewed and summarized data on reproduction vital rates of Hawaiian gallinules *Gallinula galeata sandvicensis* on the islands of Kaua’i and O’ahu by using data from 1979 to 2014. This table shows the mean, range, and standard deviation of reproduction parameters for each study, and the weighted average and standard deviation from our meta-analysis. Clutch size refers to the number of eggs laid per nest, and nest success is the proportion of nests that hatched at least one chick. Number of chicks per nest is the total number of chicks produced divided by the number of nests, including nests that failed. Number of chicks per successful nest is the total number of chicks divided by the number of successful nests (those which hatched at least one chick). Hatch rate refers to the number of chicks produced per egg among all nests. Number of chicks per successful nest is the total number of chicks produced divided by the number of nests, including nests that failed. Number of chicks per nest is the total number of chicks produced divided by the number of successful nests (those which hatched at least one chick). Study averages were derived excluding data from Gutscher-Chutz, which used different methods.

| Parameter | Mean (SD) | Range | N |
|-----------|-----------|-------|---|
| Clutch size | | | |
| Nagata (1983) | 4.56 (2.19) | 1–7 | 9 |
| Chang (1990) | 4.91 (1.27) | 2–8 | 87 |
| Gee (2007) | 6.30 (1.92) | 2–11 | 56 |
| Silbernagle (unpublished data) | 4.18 (1.67) | 1–7 | 17 |
| Gutscher-Chutz (unpublished data) | 5.57 (1.86) | 2–10 | 21 |
| Cosgrove (unpublished data) | 4.42 (1.32) | 1–8 | 45 |
| Study avg. | 5.10 (0.75) | 4.18–6.30 | 5 |
| Nest success | | | |
| Nagata (1983) | 0.42 (0.50) | — | 31 |
| Chang (1990) | 0.77 (0.42) | — | 87 |
| Gee (2007) | 0.65 (0.48) | — | 56 |
| Silbernagle (unpublished data) | 0.58 (0.50) | — | 26 |
| Gutscher-Chutz (unpublished data) | 0.20 (0.45) | — | 19 |
| Cosgrove (unpublished data) | 0.67 (0.48) | — | 43 |
| Study avg. | 0.660 (0.11) | 0.42–0.77 | 5 |
| No. of chicks/nest | | | |
| Nagata (1983) | 1.68 (2.34) | 0–8 | 31 |
| Chang (1990) | 3.42 (2.35) | 0–8 | 87 |
| Gee (2007) | 2.77 (2.58) | 0–8 | 56 |
| Silbernagle (unpublished data) | 1.58 (2.19) | 0–6 | 26 |
| Gutscher-Chutz (unpublished data) | 1.32 (1.83) | 0–5 | 19 |
| Cosgrove (unpublished data) | 1.47 (1.35) | 0–4 | 43 |
| Study avg. | 2.51 (0.94) | 1.47–3.42 | 5 |
| No. of chicks/successful nest | | | |
| Nagata (1983) | 3.71 (2.16) | 1–8 | 13 |
| Chang (1990) | 4.51 (1.53) | 1–8 | 63 |
| Gee (2007) | 4.51 (1.99) | 1–8 | 36 |
| Silbernagle (unpublished data) | 2.73 (1.56) | 1–6 | 15 |
| Gutscher-Chutz (unpublished data) | 4.4 (1.03) | 1–5 | 6 |
| Cosgrove (unpublished data) | 2.25 (1.08) | 1–4 | 28 |
| Study avg. | 3.86 (0.83) | 2.25–4.51 | 5 |
| Hatch rate (chicks/egg) | | | |
| Nagata (1983) | — | — | — |
| Chang (1990) | 0.65 (0.42) | 0–1 | 434 |
| Gee (2007) | 0.46 (0.38) | 0–1 | 364 |
| Silbernagle (unpublished data) | 0.56 (0.54) | 0–1 | 71 |
| Gutscher-Chutz (unpublished data) | 0.28 (0.34) | 0–1 | 78 |
| Cosgrove (unpublished data) | 0.34 (0.27) | 0–0.83 | 199 |
| Study avg. | 0.52 (0.12) | 0.34–0.65 | 4 |

statistically significant differences between managed and unmanaged wetlands in nest success, number of chicks per nest, or number of chicks per successful nest (Table S2, Supplemental Material). The sample size of confirmed clutch sizes and brood sizes in unmanaged habitats were insufficient for comparing clutch size or hatch rate between managed and unmanaged habitats. The data-set of Nagata (1983) was the only dataset with data gathered on unmanaged habitats. Among breeders of known age (n = 7), the youngest bred at an approximate age of 23 mo.

Information on causes of nest failure was not available for most (74%) nests in our study, which precluded analyses based on nest fate. The most frequent cause of nest failure in our review among 51 failed nests of known fate (50 in managed wetlands and 1 in an unmanaged wetland) was predation (n = 30), followed by abandonment (n = 17) and flooding (n = 4).

Nagata (1983) documented Hawaiian gallinules successfully producing two and even three broods in a year at Hamakua Marsh and private lotus farms on O’ahu. Two monitored, banded pairs of gallinules (one at Waima Valley and the other at Keawawa Wetland) had a maximum of four successful broods per year in 4 y of monitoring. We saw no evidence of reproductive senescence (reduction in brood or clutch size) for the pair at Waima Valley over 6 y of monitoring (see longevity data in next section).

Survival and movement

We documented 1,620 sightings of 423 individually marked birds over 14 y. Resighting data were collected at 14 locations on O’ahu (Figure 2). At least some monitoring for banded birds occurred in all years 2004–2017, yielding 13 annual survival intervals. Hanalei National Wildlife Refuge on Kaua’i (the only other island in the subspecies’ known range) was surveyed biannually throughout the study period for banded birds from O’ahu, but none were ever encountered. Number of marked individuals, as well as timing, frequency, extent, and methods of surveys varied substantially between wetlands (see Table S3, Supplemental Material, for summary information on resighting records). Our reduced dataset, which was limited to sightings in May and June at wetlands with the longest mark–resight records (JCNWR and Waima Valley), consisted of 637 resightings of 209 individually marked birds. All other wetlands had short (2- to 4-y) encounter histories, which seemed to be driving model overdispersion; 95% confidence intervals of yearly apparent survival for these wetlands were also uninformative when all wetlands were included in analyses (~0.1–0.99).

All candidate survival models are presented in Table 3. Our suite of yearly survival models overwhelmingly supported a model with detection varying by study year, wetland, and their interaction (Table 3). The ∆AICc value of the second-best supported model (survival varying by wetland and detection by year, wetland, and their interaction) was below 2, indicating limited evidence for a statistical difference in model support between the first two models (Burnham and Anderson 1998), and these two top models account for virtually all of the AIC weight assigned to our suite of models (Table
The third-ranked model has a \( \Delta \text{AIC}_c > 10 \), indicating substantial difference in model support. In general, models with detection varying by wetland, year, and their interaction performed best (four of the top five models). The annual apparent survival estimate for the top model was 0.663 (95% CI = 0.553–0.759), whereas wetland-specific annual apparent survival estimates for the second-ranked model were 0.565 (95% CI = 0.356–0.753) for JCNWR and 0.696 (95% CI = 0.572–0.797) for Waimea Valley. Notably, the confidence intervals of estimated annual apparent survival in these two subpopulations overlap. The null model (constant \( \phi \) and \( p \)) had the lowest ranking. Estimated detection rates varied across wetland-years from near 0 (0.5 \( \times 10^{-15} \)) to 1, with detection rates at Waimea Valley typically much higher than those at JCNWR. Our null model for detection estimated an overall detection rate of 0.496.

Neither global tests nor individual component tests of the assumptions of CJS models yielded significant p-values in U-CARE for either reduced dataset. The estimated \( c \) for our general model using the reduced dataset was 1.317, whereas the p-value of its deviance rank was 0.092. Generally, \( c \) values close to 1 and nonsignificant deviance rank p-values indicate that the model is a good fit for the data. These values indicate that our yearly model had acceptable goodness of fit with respect to our dataset. The oldest individual gallinule in our dataset was found dead in 2013 and had been banded in 2005 at the age of 28–35 d. Its estimated age was thus 7 y and 8 mo.

No birds banded on O‘ahu have ever been detected on Kaua‘i since the start of mark–recapture studies in 1979. Our own monitoring, combined with citizen-science resighting data, detected only three confirmed movements between wetlands (treating a wetland complex as a single wetland) on O‘ahu. One adult bird (USGS 107639253, YA:WL) banded on September 23, 2005, at JCNWR was seen on January 29, 2008, at Pearl Harbor National Wildlife Refuge (~36-km straight-line distance; Figure 3). A first-year bird (USGS 119687856, HA:PO) banded at Keawawa Wetland on July 2, 2014, was seen on January 22, 2015, at Enchanted Lake (10 km straight-line distance). A third bird, banded as an adult on June 10, 2015, at Turtle Bay Resorts’ Arnold Palmer Golf course (USGS 119687902, WA:RB) was recovered dead on July 13, 2016, at Olomana golf links (~47-km straight-line distance). Unconfirmed reports (for which reported bands were incomplete, or for which no photographic evidence could be provided) include a bird moving from JCNWR to a drainage ditch in Haleiwa in 2015 (20-km straight-line distance), a bird banded at Keawawa Wetland seen in Kamilolui Valley in 2015 (~2-km straight-line distance), and a bird banded at Waimea Valley seen at Olomana golf links in 2016 (45-km straight-line distance; Figure 3).

We found no information on postfledging (juvenile) survival rates in unpublished studies. Two studies in our meta-analysis (Chang 1990; Gee 2007) included repeated observations of broods across time from which rough estimates of survival can be derived. Chang (1990) observed that 28 (41.7%) of 67 chicks observed from a blind throughout the fledging period (50–60 d; Bannor and Kiviat 2002) at JCNWR survived from hatch to fledging. Gee (2007) observed much lower survival (37% of 162 chicks) across the same time frame at Hanalei National Wildlife Refuge on Kaua‘i.

**Discussion**

This study presents the first survival rate data of which we are aware for the Hawaiian gallinule and a large expansion on what is known about their reproductive success. Data from this study will enable quantification of extinction risk via population viability analysis for this subpopulation.
subspecies across its current range, a management priority according to the USFWS’s recovery plan for Hawaiian waterbirds (USFWS 2011). Our meta-analysis illustrates the range and central tendency in several vital rates for Hawaiian gallinules, synthesizing unpublished information from several studies from 1979 to 2014. In our analysis of pooled data, we found clear differences in several reproductive parameters between Hawaiian gallinules on O’ahu and Kaua’i, with smaller clutches but greater hatching rates on O’ahu. We also generated an overall estimate of annual apparent survival for the subspecies on O’ahu by using more than 600 resightings of 209 individuals at two wetland sites.

We found that Hawaiian gallinules have relatively small mean and range of clutch sizes compared with the North American subspecies Gallinula galeata cachinnans (e.g., mean = 7.9%, n = 2685; Greij 1994) showing greater similarity to gallinules at tropical latitudes, for example, Gallinula angulata (mean = 5.0, n = 55; Taylor and van Perlo 1998). This is consistent with the general observation that clutch sizes are directly related to latitude, where higher clutch sizes are observed in temperate regions at high latitudes and smaller clutch sizes are observed in tropical regions at low latitudes (Cody 1966; Rose and Lyon 2013), especially in low-elevation habitats (Balasubramaniam and Rotenberry 2016). Small clutch sizes of Hawaiian gallinules may also be due to a suite of evolutionary or ecological island effects (Lack 1947, 1970; Cody 1966; Klomp 1970; Frankham 1998). Higher clutch sizes on Kaua’i may be the result of brood parasitism, a prominent behavior in common moorhen Gallinula chloropus (Gibbons 1986) that might be facilitated by the high breeding densities of Hawaiian gallinules at Hanalei National Wildlife Refuge (J.C. and K.U., personal observations).

Mean hatch rate in this study (mean = 50% for meta-analysis, Table 2; mean = 43% for pooled data in Table S1, Supplemental Material) was much lower than that reported by Greij (1994) in a large study of common gallinules in North America (1,974; mean = 80.2%, n = 2,685 nests) and in a report for G. tenebrosa in Australia (55.5%; Marchant and Higgins 1993). Nest success of Hawaiian gallinules in both our meta-analysis and pooled data was similar to that reported by Greij (1994) in North America (mean = 64.1%, n = 968) and G. chloropus in Great Britain (65.3%, n = 1,154; Cramp and Simmons 1980), but higher than that observed by Jamieson et al. (2000) in nests of G. angulata in Namibia (58% failure, n = 33).

O’ahu’s higher mean number of chicks produced per nest and chicks per successful nest in our pooled dataset came as a surprise, given the higher clutch sizes on Kaua’i and the absence of one major mammalian predator, the small Indian mongoose. The small Indian mongoose is common on O’ahu but rare or not established on Kaua’i (Hays and Conant 2007; USFWS 2011). Because of the scarcity of data on posthatching survival rates, however, the effect of differences in clutch sizes and hatching rates on recruitment and population growth is unknown. Examining our meta-analysis (Table 2), it seems that this higher number of chicks is driven mostly by data from Chang (1990), who had a large sample size and the highest mean number of chicks per nest and chicks per successful nest; these data came from managed habitats and so contribute to a trend in
our estimates of likely being optimistic for subpopulations in nonmanaged habitats.

The estimates of Chang (1990) and Gee (2007) of chick survival to fledging among Hawaiian gallinules on O’ahu may fit well with observations of common gallinule *G. galeata cachinnans* chicks in the southern United States, for which chick mortality was estimated at >40% in the first 10 d posthatch (Miller 1946; Bell 1976). According to the review by Greij (1994), Helm (1982) and Matthews (1983) observed reductions in brood size across a 45-d period posthatch that were similar to values observed here in Hawaiian gallinules (~45% survival). Although the difficulty of marking and resighting chicks is an obvious factor in poor understanding of this life stage, it remains an important research priority. This low chick survival may be evidence of a limiting factor in the population regulation of Hawaiian gallinules; accordingly, management actions focused on improving chick survival are a reasonable priority for wetland managers in Hawai'i. Removal, reduction, and exclusion of predators in refuges is likely the most direct approach to increasing chick survival (USFWS 2011; VanderWerf 2012).

Ostensibly high chick mortality in Hawaiian gallinules matches the assertion of Greij (1994) that multiple broods are an important part of population management in common gallinules. Indeed, we observed consistent multiple clutching in two observed pairs with a maximum of four broods in a year, and Nagata (1983) reported frequent double- and triple brooding at other wetlands on O’ahu. Byrd and Zeillemaker (1981) also observed evidence of multiple broods in a year, noticing family groups with young at two or more distinct stages of development. Bannor (1998) observed a pair of common gallinules in a zoo in Florida hatch five broods in 1 y under conditions of supplemental feeding, and Siegfried and Frost (1975) observed common moorhen hatch 33 and 32 broods over a 48-mo period, also with supplemental feeding, in South Africa. Given that DesRochers et al. (2010) found that Hawaiian gallinules are not food limited on O’ahu and that conditions in Hawaiian wetlands are highly consistent year-round, our observation of widespread and frequent multiple brooding is intuitively understandable.

The lack of observed differences in reproductive parameters between managed and unmanaged wetlands in our pooled dataset may be an artifact of the small sample size for unmanaged wetlands (*n* = 22) compared with managed wetlands (*n* = 230). Endangered Hawaiian waterbirds can have large interannual and intersite variation in vital rates, particularly for hatch-year birds (Reed et al. 2015), and we cannot determine whether differences observed were due to chance differences in interyear and intersite variation. We acknowledge the possibility that sites not specifically managed for endangered waterbirds might still include activities that decrease predation, such as the presence of guard dogs that do not attack waterbirds (as in the lotus farms). Some site-specific management activities, such as water level controls for aquaculture (as in watercress and shrimp farms), might also reduce nest flooding, which was a notable source of clutch failure for known-fate nests in this study. Nagata (1983) who did much of her work in unprotected areas and a refuge (Hamakua Marsh) at which predator control may have been limited at the time of the study, showed lower nest success and than other studies, reinforcing the notion that our general estimates may be somewhat optimistic for unmanaged wetlands. Unfortunately, we do not yet know what life stage most limits population growth; determining this by using population modeling would provide insight for how to focus management effort and funding on Hawaiian wetlands (e.g., Crouse et al. 1987; Beissinger and Westphal 1998; Fefferman and Reed 2006). In general, wetland managers in Hawai'i would benefit from studies that focus on collecting similar baseline vital rate info in unmanaged habitats for purposes of comparison.

Reported age at first breeding for *G. chloropus* in the literature is 1 y (Taylor and van Perlo 1998). Our youngest breeder for the Hawaiian subspecies was almost 2 y old, but our small sample size of known-age breeders (*n* = 7) does not indicate how representative this observation is. The oldest known bird in our dataset, 7 y and 8 mo, was younger than the oldest reported common gallinule (9 y and 10 mo; Clapp et al. 1982). This may be due to comparatively limited sampling of Hawaiian birds, or it could represent a difference for island birds. Longevity data are an important part of population-projection models, which in turn help guide management by estimating the level of risk faced by different populations (Morris and Doak 2002). Continued monitoring of banded Hawaiian gallinules on O’ahu is necessary to gain a more accurate understanding of the distribution of life spans among birds in managed and unmanaged wetlands.

Our resighting database is the only published account of banding, resighting, and recovery of Hawaiian gallinules of which we are aware. The high performance of survival rate models that varied detection parameters by wetland, year, and their interaction reflects the variation of monitoring effort and ease of detection between wetlands and across time, a product of ad hoc research efforts by researchers and institutions. Gallinules at JCNWR are behaviorally cryptic due to limited human disturbance and have flight initiation distances in excess of 75 m (C.B.v.R., personal observation). This makes resightings at JCNWR more difficult than at wetlands such as those at Waimea Valley, where birds have frequent exposure to humans, resulting in tolerance of human proximity; they occasionally even approach humans for food. Habitat structure in Waimea Valley, a botanical garden, is also substantially different than that at JCNWR, with more open water areas and paved pathways where gallinules are easily spotted. These differences are likely the strongest drivers of differences in detection between these wetlands. Although a by-wetland annual apparent survival model performed as well as the top model, the 95% confidence intervals of annual apparent survival between the two wetlands overlapped, indicating that the effect of wetland setting on apparent survival is trivial when comparing these two wetlands. Given that the two wetlands included in our
reduced dataset (the only ones with sufficient data available) were both managed wetlands, we also have no information on gallinule survival rates outside of managed areas. Such information will be important for understanding the effect of prevailing management strategies on adult survival rates in this subspecies.

Our resighting data set is missing a potentially important period in the gallinule life cycle when survival rates are lower; specifically, the first ~40 d of life between hatching and the point when young birds are large enough to band (Fredrickson 1971). In a study of a different species of endangered Hawaiian waterbird, the Hawaiian stilt Himantopus mexicanus knudseni, Reed et al. (2015) found that this age class had the highest mortality rate. Although our literature research yielded some limited information on chick survival in Hawaiian gallinules, this information is crucial for future work, not only for its likely importance to population dynamics but also because chick survival is probably among the easiest vital rates to influence via management. Trapping and exclusion of invasive mammalian predators are a key part of management for Hawaiian waterbirds on wildlife refuges on O‘ahu, where they are thought to reduce predation rates on nests and chicks (USFWS 2011). Better knowledge of the extent to which such management improves this vital rate, and the impact this vital rate has on overall population trends, would be instrumental in improving conservation of this subspecies. The impacts of avian botulism on Hawaiian gallinules are virtually unstudied, although the incidence in this subspecies seems rare (K.U., personal observation). It is also unknown whether botulism has different impacts on juvenile vs. adult gallinules, so a major research priority is monitoring incidence of the disease across life stages, to elucidate which parts of the life cycle it impacts most severely.

Although our goodness-of-fit tests indicated that our dataset meets expectations determined by the assumptions of the CJS model, the limitations and asymmetries of this dataset (see Table S3, Supplemental Material) prevented us from including most of our 14 study sites because the sparseness and short duration of their encounter histories led to overdispersion. The high performance of our null model of annual apparent survival (ϕ constant across both wetlands) is in line with conservative thinking in model selection, particularly where the number of data points per parameter (in this case, encounter histories, n = 26) is limited (Harrell 2001). As Beissinger and Snyder (2002) noted, the most complex model is not necessarily the most useful if there is no reliable biological interpretation, and in this context our null model for annual apparent survival, although it does not provide information on annual or habitat-based differences, is our most credible parameter estimate. This estimate can accordingly be used for population viability analysis and for comparative work as data on survival in unmanaged habitats become available.

Little is known about the movement rates or patterns of Hawaiian gallinules (Dibben-Young 2010), although they are reputed to be highly sedentary (Shallenberger 1977). Dispersal beyond survey sites can cause underestimation of survival rates (Koenig et al. 1996), raising the potential concern that dispersal has biased estimates in our study. Any impact of dispersal on apparent survival rates is likely to be higher in data from earlier in this study (before 2014), when few wetlands were monitored. Banding and surveying for Hawaiian gallinules has occurred opportunistically for the last decade, typically with periods where a cohort of birds was banded, monitored briefly, and then not systematically surveyed for several years. In addition, bird behavior affecting detectability apparently varies between wetlands; DesRochers et al. (2008) observed a greater proportional response to call playback at sites with more birds. Our mark–recapture study showed minimal evidence of movement (three confirmed movements), despite exhaustive surveys of 14 sites for four consecutive years, and regular monitoring of four sites (Waimea Valley, JCNWR, Pearl Harbor NWR, and Hamakua Marsh) for 13 y. This corroborates findings by van Rees et al. (2018) that movement may be severely limited in Hawaiian gallinules, reducing the possibility that dispersal has severely impacted our survival and detectability estimates, but reinforcing the notion that habitat connectivity may be a risk factor for subspecies’ population dynamics. The problem of poor detectability remains, however, and more in-depth studies on gallinule movement behaviors are necessary. Radiotelemetry studies may be a feasible alternative, although given our low rates of observed movement a very large sample size would be required. A better understanding of gallinule movement behavior would help managers better predict the effects of habitat management actions (e.g., will birds disperse under unfavorable habitat conditions) and would reveal which management units on the island are connected by dispersal between subpopulations.

All of the resighting data analyzed in our reduced dataset came from wetlands that were under active and ongoing habitat management (predator control and removal of invasive plants), and although most of Hawaiian gallinules are currently found in protected areas, our estimates may be optimistic for unmanaged wetlands. Regular and systematic surveys for banded birds at a larger number of wetland sites would make substantial and timely contributions to current knowledge of survival and movement rates of Hawaiian gallinules. The current cohort of banded individuals thus represents a new and unique opportunity to collect valuable information on the behavior and survival of these birds, but consistent, long-term follow-up is essential to collecting these data. Marking and monitoring of fledglings will also be of value, because poor knowledge of survival rates during this life stage is a major gap in our understanding of the life cycle of the Hawaiian gallinule. Increased nest searching and monitoring, as well as banding and resighting in unmanaged habitats will also be important to quantify the impacts of vegetation management and predator control, the two most commonly used management strategies, on gallinule vital rates and population dynamics.
Supplemental Material

Table S1. We reviewed unpublished data on the reproduction vital rates of Hawaiian gallinules *Gallinula galeata sandvicensis* collected on the islands of Kaua‘i and O‘ahu from 1979 to 2014. We pooled these data to generate overall and by-island estimates of mean vital rates, for cases when more general information with higher sample size is preferable. $N =$ number of nests. The last column is comparative data from a published study on Kaua‘i (data not included in our study; Byrd and Zeillmaker 1981). Dashes indicate information not available or not estimated; asterisk (*) indicates a statistically significant difference in means between islands ($P \leq 0.05$).

Table S2. We reviewed unpublished data on the reproduction vital rates of Hawaiian gallinules *Gallinula galeata sandvicensis* collected on the islands of Kaua‘i and O‘ahu from 1979 to 2014. We pooled these data to compare reproductive parameter values between managed and unmanaged habitats. $N =$ number of nests. Dashes indicate information not available or not estimated; we detected no statistically significant differences between any of the tested vital rates. Sample sizes in unmanaged wetlands were insufficient for hypothesis testing of clutch size and hatch rate.

Table S3. Distribution of banding effort, survey effort, and resighting data among wetlands where Hawaiian gallinules *Gallinula galeata sandvicensis* were banded and monitored on O‘ahu, Hawaii for all years in our resighting database (2004–2017). Because of sparse, limited data and violations of model fit when including data from all other wetlands, only survival data from James Campbell National Wildlife Refuge and Waimea Valley were used in our final analyses. In addition, to meet the assumptions of the Cormack–Jolly–Seber model, we restricted these data only to resightings in May and June. Accordingly, only 637 of the resightings shown below were used in our final analysis. Banded Individuals describes the number of individual birds banded at each wetland and years of monitoring describes the number of years in which sites were revisited for resightings. The number of resightings at each wetland includes those resightings of birds banded at that wetland as well as immigrants banded at other wetlands. Notably, years of monitoring and number of banded individuals vary largely between groups.

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