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Management and Conservation Article

Evaluating if Energy and Protein Limit Abundance of Hawaiian Moorhen

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ABSTRACT Food abundance can affect a species' distribution. In many studies of potential food limitation, researchers focus on carrying capacity estimates during the nonbreeding season for temperate species consuming a fixed food source. Estimates of energetic carrying capacity for year-round breeders feeding on a replenishing resource would be more difficult and require much data. To determine whether gathering detailed information on year-round carrying capacity would be an important investment, we conducted an assessment to determine whether there was evidence that energy or protein might limit numbers of the tropical, endangered Hawaiian moorhen (*Gallinula chloropus sandvicensis*). We compared observed numbers of moorhen at 15 Oahu, Hawaii, USA, wetlands with predicted numbers based on measured energy and protein in food plants and abundance of these food plants in each wetland and on estimates of energy expenditure of moorhen. We made comparisons assuming moorhen are limited by their ability to metabolize food plants, by competition for food, and by estimated costs associated with reproduction. We also compared ranked moorhen abundance and density with ranked energy and protein under different wetland management regimes. Energy values consistently overestimated expected numbers of Hawaiian moorhen at wetlands except for one wetland location (predicted, 3803 ± 4856; observed, 6.2 ± 10.8). In addition, we detected no significant relationship between moorhen abundance and measures of energy (all $r^2 = 0.02$–0.73, all $P > 0.1$) or protein abundance (all $r^2 = 0.08$–0.50, all $P > 0.3$). This lack of relationship held once we controlled for wetland area or when we considered whether wetlands were managed for waterbirds. Hawaiian moorhen on Oahu did not appear to be limited by energy, nor did they appear to select sites based on energy or protein, in contrast to many studies relating animal numbers to energy in nonbreeding situations. Consequently, we suggest that researchers and managers explore other potentially limiting factors for Hawaiian moorhen.

KEY WORDS herbivory, nutritional ecology, population, population limitation, rails, waterbird management.

Understanding what limits species abundances and distributions is a question in population and community ecology, biogeography, and conservation (e.g., Lack 1954, Whittaker et al. 2005, Beissinger et al. 2006). The prevalent approach to understanding species' distributions is to quantify local or landscape characteristics thought to be important to species occurrence (e.g., local vegetation cover) and use statistical tools to identify correlates of presence or abundance at a site (e.g., references in Scott et al. [2002]). Results from this type of analysis also can have practical applications, such as identifying biodiversity hot spots (Eken et al. 2004), advising habitat restoration (Whited et al. 2000, Newbold and Eadie 2004), predicting invasibility of translocated species (Thuiller et al. 2005, Le Maitre et al. 2008), and predicting effects of climate change (Lawler et al. 2009). Concerns have been raised over this habitat- or niche-based approach, however, such as mismatching ecological processes with sampling scales, misunderstanding the ecological processes causing observed patterns, and models often failing to elucidate nonlinear patterns (Heglund 2002, Huston 2002). Consequently, Morrison (2001) and O'Connor (2002) proposed a fundamental change to how researchers model site occupancy and abundance of species to focus on determining factors that limit local population size, of which habitat constraints are just one possible suite of factors. Other potential constraints include quality of food resources, mate availability, biotic interactions (e.g., competition), and abiotic factors (Grinnell 1917, Newton 2003, Pearson and Dawson 2003).

One way to model population sizes as a function of constraining factors is using behavior-based models, which focus on individual constraints within an environment (Sutherland 1996). Behavior-based models of birds typically have been used to predict population responses to changes in food abundance and competition in nonbreeding populations of diet specialists. For example, individual energy requirements, intra- and interspecific competition, energy intake, and food value from grazing accurately predicted bean goose (*Anser fabalis*) and Eurasian wigeon (*Anas penelope*) population sizes (Sutherland and Allport 1994). Similarly, energetic carrying capacity has been calculated for management of game species (Anderson and Smith 1999, Guthery 1999, Brasher et al. 2007) or for species of conservation concern (Goss-Custard et al. 2002, Masero et al. 2008).

In addition to energy, nutritional quality of food, such as amounts of protein, fiber, or plant defensive compounds could limit population size (Hobbs and Swift 1985, DeYoung et al. 2000, Servello et al. 2005). However, the potential for noncaloric nutrient limitation has been largely ignored in vertebrates (Frederick et al. 1987). Although there are notable exceptions such as the red grouse (*Lagopus l. scotica*), which might be limited by phosphorus content in its primary food (Moss 1969). There also is evidence that calcium levels in soil influence distribution and abundance of ring-necked pheasants (*Phasianus colchicus*; Dale 1954, Anderson and Stewart 1973), wild turkeys (*Meleagris gallopavo*; Leopold and Dalke 1943), and migrating black brant (*Branta bernicla nigricans*; Lee et al. 2004).

Our goal was to determine whether food energy and protein within wetlands influences abundance of an

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endangered avian herbivore, the Hawaiian moorhen (*Gallinula chloropus sandvicensis*). Investigating how abundance relates to aspects of physiology can provide greater understanding of species–habitat relationships, and such is the case with the Hawaiian moorhen (Artacho et al. 2007). Currently, Hawaiian moorhen only number in the hundreds range-wide, and it is unknown what limits their distribution or population size (Reed et al. 2007, DesRochers et al. 2008). Identifying limiting factors would help managers improve conservation efforts for this species; identifying and ameliorating population limitations is necessary before delisting Hawaiian moorhen could occur (Griffin et al. 1989, U.S. Fish and Wildlife Service 2005). Our primary objective was to relate Hawaiian moorhen abundance to measures of energy and protein in each food plant species based on density of each plant in 15 wetlands on Oahu, Hawaii, USA. We wanted to calculate an energetic carrying capacity for moorhen but that currently is not feasible. Energetic carrying capacity in birds is typically calculated for temperate species in the nonbreeding season with a standing food crop that is depleted over time (e.g., Anderson and Smith 1999, Goss-Custard et al. 2002). However, Hawaiian moorhen breed year-round, and their food plants can grow year-round, particularly in managed wetlands, so food resources are replenished over time at unknown and variable rates, depending on management activities (Shallenberger 1977, Byrd and Zeillemaker 1981, Griffin et al. 1989). Furthermore estimating energetic carrying capacity requires knowing metabolizability of various diet items for moorhen. Gathering this information would be time-consuming and costly.

Consequently, our goal was to determine, using currently available information and estimated relationships, if gathering detailed information on metabolizability would be important for future Hawaiian Moorhen management. We tested a suite of hypotheses about the possible relationship between Hawaiian moorhen abundance and food resources. First, we tested the hypothesis that energy limits moorhen numbers at wetlands in the context of different assumptions: moorhen numbers are limited by a combination of 1) their estimated ability to metabolize food, 2) competition with Hawaiian coots (*Fulica alai*) and ducks (*Anas* spp.), and 3) energetic requirements associated with reproduction. Second, we tested the hypothesis that even if moorhen numbers are not limited by energy abundance at wetlands, it is still affecting settlement decisions. That is, we predicted that Hawaiian moorhen abundance would be associated with ranked estimates of metabolizable energy at wetlands after discounting for competition with coots and ducks. We also made this same comparison for moorhen abundance and dietary protein.

STUDY AREA

Our 15 study wetlands were on the island of Oahu. The sites were low-elevation, coastal, freshwater wetlands except for some wetland impoundments (salinity >30 parts per thousand) at James Campbell National Wildlife Refuge (Kii) and Hamakua, which is a brackish wetland. Wetland plant communities were dominated by emergent vegetation. Wetlands varied from sites managed for endangered waterbirds ($n = 6$) to other sites ($n = 9$) such as golf course ponds managed for aesthetics or naturally occurring ponds with no management activity (see DesRochers et al. [2008] for a detailed description of the wetland study sites).

METHODS

We estimated Hawaiian moorhen population size at these wetlands using call-broadcast surveys from a previous study (DesRochers et al. 2008) done from June to July in 2006, the same time period as when we gathered wetland plant data for the nutritional analysis. For the other waterbird (Hawaiian coot and duck species) abundances, we used the 2006 summer adult numbers from Hawaii's Bi-annual Waterbird Survey database (available from the Hawaii Biodiversity and Mapping Program at the University of Hawaii at Manoa, Manoa, HI). To determine whether our bird survey numbers were representative of the standing summer time population sizes, we calculated 95% confidence intervals using summer numbers of each species observed from 1988 to 2007. As an additional evaluation, we compared summer and winter numbers of all 3 waterbird species at 14 of our study sites. However, annual waterbird surveys were not conducted at one of the wetlands we included. We mapped vegetation communities of the wetlands to quantify the area covered by each food plant by sketching visual estimates of coverage of each plant species within a wetland and then using ImageJ 1.38× (Abramoff et al. 2004) to quantify percent area covered so that we could calculate area covered by each species. More intrusive sampling of vegetation communities was not possible due to restrictions on entering wetlands, to reduce risk of disturbing endangered waterbirds. We did, however, compare our visual estimates with dispersion of the entire communities of emergent wetland vegetation to determine if our estimates were reasonable. To determine energy and protein of food plants, we harvested above-ground tissue from 11 food plant species known to be consumed by Hawaiian moorhen at Kii and Waimea Valley (both on the north shore of Oahu). Food plant species we selected represent a subset of the total wetland plant communities. See DesRochers et al. (2009) for specific harvest protocol, macronutrient analysis, energy density, and proximate protein content of each plant species. In brief, we harvested all plant parts (e.g., leaves, seeds, or stems) that moorhen were likely to consume based on previous observations of foraging moorhen. We collected these parts from randomly placed 0.25-m^2 plots, and where possible, we placed sample plots of each species in separate wetland impoundments at Kii. We harvested common waterweed (*Egeria densa*) only at Waimea Valley. From the food plant community surveys and macronutrient analyses, we estimated energy density (kJ/m^2) of each plant species based on the amount of plant material remaining/m^2 postdrying and then calculated gross energy and total protein content of each wetland.

The second part of our analysis required us to estimate energetic requirements for free-living adult Hawaiian moorhen. We used the allometric equation for avian field metabolic rate (FMR) from Nagy (2005): FMR = 10.5 × $M_b^{0.681}$ kJ/day, where M_b is body mass in g ($r^2 = 0.94$, $n = 95$ species). We also calculated FMR for 2 avian herbivores that co-occur with moorhen, the Hawaiian coot (Pratt and Brisbin 2002) and a hybridized *Anas* duck of mixed parentage from Hawaiian ducks (*A. wyvilliana*) and mallards (*A. platyrhynchos*; Engilis et al. 2002). The Hawaiian coot particularly is relevant because coots regularly exclude moorhen from foraging areas during breeding (M. Silbernagle, U.S. Fish and Wildlife Service, personal communication). Hawaiian moorhen weigh, on average, 350.7 ± 50.0 g (SD; $n = 82$; DesRochers et al. 2010), coots weigh 533.7 ± 77.6 g ($n = 231$, U.S. Fish and Wildlife Service and A. Dibben-Young, Nēnē O Moloka'i, unpublished data), and mean body mass of male and female adult hybrid ducks is 870 g (A. Engilis, University of California, Davis, personal communication).

To test the hypothesis that energy limits Hawaiian moorhen, we discounted gross wetland energy (kJ) value of each plant species by a minimum as well as a maximum metabolizability value, discounted these reduced energy values for each wetland by amount of energy required by Hawaiian coots and hybrid ducks in 1 month (sensu Anderson and Smith 1999) and then subtracted amount of energy that moorhen require for reproduction based on reproductive data from published literature. Because we did not know species-specific metabolizability of various food types for Hawaiian moorhens, Hawaiian coots, or hybrid ducks, we discounted gross energetic values of seeds by 59% (Karasov 1990) for the minimum metabolizability analysis as well as by 78% (Castro et al. 1989) for the maximum metabolizability analysis. Similarly, we discounted values of plant tissues by 37% (Castro et al. 1989) and 62% (Kaminski and Essig 1992), respectively. Energy estimates for large-seeded sedge species were additionally discounted because it has been observed for other bird species that only approximately 50% of the seeds of these sedge species typically pass through organisms without being digested (Hoffman and Bookhout 1985, Dugger et al. 2007). As a result, we halved the gross energy values of saltmarsh bulrush (*Bolboschoenus maritimus*) and California bulrush (*Schoenoplectus californicus*) before calculating the minimum and maximum metabolizable energy of our study wetlands. Taxonomic nomenclature of vegetation follows Erickson and Puttock (2006).

We then calculated amount of energy required to support the number of coots and ducks for 1 month that were observed at our sites during the 2006 summer waterbird survey:

$$E_c = ME_{\text{min. } or \text{ max.}} - 30 \times [\text{no. coots} \times FMR_c + (\text{no. ducks} \times FMR_d \times 0.4)] \quad (1)$$

where ME_x is total metabolizable energy (kJ) in a wetland for minimum and maximum metabolizability estimates, FMR_c is FMR of coots, and FMR_d is FMR of ducks, where we calculated FMR using Nagy's (2005) equation. Plant material only comprises approximately 40% of Hawaiian duck diets, so we assumed that this was true for the *Anas* hybrids, which resulted in discounting duck FMR by 40% (Engilis et al. 2002).

Finally, we calculated the amount of energy moorhen required for reproduction. Our added assumption was that Hawaiian moorhen were selecting sites with sufficient resources to lay and rear an average clutch of eggs through fledging (7 weeks; Helm 1982), even though this takes >30 days. Specifically, we calculated energetic cost assuming that 1) moorhen, on average, lay a clutch of 5.2 eggs; 2) 69% of the female population breeds; 3) 71% of eggs hatch; and 4) 42% of chicks survive to fledging (Nagata 1983, Chang 1990). We calculated in the manner of King (1973) the energetic cost (kJ) of producing a clutch of 5.2 eggs (E_{egg}) as

$$E_{egg} = [E_M \times E_{En} \times (100/E_{PE})] \times 5.2, \quad (2)$$

where E_M is fresh mass of a moorhen egg (unknown for Hawaiian moorhen, but for the European subspecies [*G. c. chloropus*] it is 24.9 g; Wood 1974), E_{En} is energetic value of an egg (28.5 kJ/g wet wt; Carey et al. 1980), and E_{PE} is efficiency of egg production (cost of producing an egg) from body reserves (73%; King 1973). Because we were unable to determine sex ratios of moorhen at our wetlands, we assumed a 1:1 sex ratio. We then calculated growth rate of Hawaiian moorhen chicks based on chick growth data from Karhu (1973) for the European subspecies. As a result, we expect Hawaiian moorhen growth to follow the relationship $y = 0.195x - 0.0143$ ($r^2 = 0.96$), where y is percentage of assimilated adult body weight on day x. We used a daily survival rate of 0.982 estimated from Chang (1990). We then calculated total energetic cost of reproduction (egg production and growing chicks to fledging age) at a wetland (E_r) as

$$E_r = (F \times 0.69 \times E_{egg}) + \left[\sum_{day\ i=0}^{38} (FMR_{ch,i} \times (\text{no. chicks} \times 0.982^i) \right], \quad (3)$$

where FMR_{ch} is FMR of a chick age i based on body mass determined from the growth model, and F is number of females determined from our field data. From this, we calculated the number of adult moorhen that a wetland could support for 1 month based on estimates of minimum and maximum metabolizable energy after competition and reproduction as

$$\text{No. moorhen}_{c+r} = \frac{ME_{\text{min } or \text{ max}} - (E_c + E_r)}{(30 \times FMR_m)}, \quad (4)$$

where FMR_m is FMR of moorhen. We then compared the observed number of moorhen from field surveys to the maximum number of moorhen that we predicted that each wetland could support.

Finally, to determine whether energy value might be an important cue to site selection even if it does not limit

Table 1. Gross energy (kJ/m^2) and protein (g dry matter/m^2) density from food plants consumed by Hawaiian moorhen in wetlands on Oahu, Hawaii, USA. Data are based on energy density and protein values reported in DesRochers et al. (2009). We sampled plants during July 2006 at James Campbell National Wildlife Refuge, Kuhuku except for Common Waterweed, which we collected at Waimea Valley, Haleiwa, Oahu, Hawaii.

Species	Energy	SD	Protein	SD
Common waterweed	2,131.5	597.2	26.1	7.3
Common cattail (*Typha latifolia*)	2,054.0	1,941.1	16.5	15.6
Pickleweed (*Batis maritima*)	1,624.9	549.9	18.1	6.1
California bulrush	1,497.6	1,165.9	6.2	4.8
Manyspike flatsedge (seeds)	1,333.5	571.9	6.8	2.9
Saltmarsh bulrush	1,243.5	1,053.5	6.1	5.2
Java sedge (*Cyperus javanicus*)	1,200.4	919.2	5.2	4.0
California grass (*Urochloa mutica*; plants <10 cm)	897.2	420.5	6.7	3.1
Bermuda grass (*Cynodon dactylon*)	715.9	329.9	4.2	1.9
Echinochloa spp.	585.3	265.5	4.0	1.8
Manyspike flatsedge (young leaves)	330.3	205.5	3.4	2.1

Hawaiian moorhen population size, we looked for a relationship between the ranked observed number of moorhen and ranked no. moorhen$_{c+r}$ for wetlands using the minimum metabolizable energy values. We also made this comparison for ranked values of the estimated amount of protein in wetlands and then made both of these comparisons controlling for area and then for both managed and unmanaged wetlands. Protein value data came from DesRochers et al. (2009) from the same plant samples that provided energy density data.

RESULTS

Mean number of Hawaiian Moorhen we detected was 6.2 ± 10.8 (SD) adults per wetland (median = 3, range = 0–40, mean density: 2.0 ± 6.0 birds/ha), with 4 wetlands supporting no moorhen despite presence of food resources. Mean abundances of all 3 waterbird species at our study sites fell within the 95% confidence intervals for observed abundances during summer waterbird surveys from 1988 to 2007 (moorhen: 6.2 ± 10.8 [$\bar{x} \pm$ SD] this study, 95% CI = −14 to 21, coots: 27.3 ± 47.1, −74.5 to 129.0, ducks: 8.2 ± 11.0, −15.5 to 32), and mean numbers of all 3 waterbird species did not vary between seasons during the same 20-year period (moorhen-summer: 3.7 ± 8.0, moorhen-winter: 4.1 ± 7.9, paired *t*-test: $t_{13} = -1.0$, $P = 0.3$; coots-summer: 27.3 ± 47.1, coots-winter: 25.3 ± 47.1, $t_{13} = 0.8$, $P = 0.4$; ducks-summer: 8.2 ± 11.0, ducks-winter: 12.4 ± 19.6, *t*-test: $t_{21} = -0.6$, $P = 0.6$; D. W. DesRochers, Tufts University, unpublished data). Wetlands supported 1–10 species of food plants; 8 wetlands supported only one species of food plant. On average, food plant species provided 1,237.6 ± 577.1 kJ of gross energy/m^2 and 9.3 ± 7.1 g dry protein/m^2, although there was tremendous variability among food plant species (Table 1), and wetlands supported 125,867 ± 164,285 MJ of energy (Table 2) and 983 ± 1324 kg of protein. For a free-living, adult Hawaiian moorhen, FMR = 567.9 kJ/d, Hawaiian coot FMR = 755.9 kJ/d, and hybrid duck FMR = 1,054.4 kJ/d. Based on energy content considering maximum estimates of metabolizability, competition, and estimated energetic costs associated with reproduction, all but one wetland, regardless of management status, is expected to support more adult moorhen than observed (predicted, 3803 ± 4856; observed, 6.2 ± 10.8; Fig. 1; we present only values based on max. metabolizability estimates because values based on min. metabolizability estimates showed a nearly identical pattern). Kaelepulu was predicted to support no moorhen once we discounted energy for competition and reproduction, but in reality, we observed 14 adult moorhen at this wetland. Waihee was predicted to support 6 adult moorhen, and we observed 3 during surveys. In addition, moorhen abundance and density were not associated with energy (all $r^2 = 0.02$–0.73, all $P > 0.1$) or protein (all $r^2 = 0.08$–0.50, all $P > 0.3$) even when considering whether sites were managed for waterbirds.

DISCUSSION

Effective management for the endangered Hawaiian moorhen requires information on factors that limit its numbers. Results suggest that current moorhen populations on 15 Oahu wetlands were not energy-limited. This lack of relationship is further supported by the observation that wetlands managed for endemic waterbirds, such as James Campbell National Wildlife Refuge, also supported fewer moorhen than our energetics estimates suggested could be supported (U.S. Fish and Wildlife Service 2005). Our expectation was that the fit between energetics and bird numbers would be closer for managed wetlands because managed wetlands are controlled for predators (e.g., black rats [*Rattus rattus*] and small Indian mongooses [*Herpestes javanicus*]) that might limit moorhen numbers. In addition, we wondered how much energy would be left over for moorhen given minimum metabolizability, competition, and reproduction assuming that the only plant present at wetlands was a monoculture of the food plant with the lowest energy value per area (in this case, young seedlings of manyspike flatsedge [*Cyperus polystachyos*], 330.3 kJ/m^2; DesRochers et al. 2009). In this minimized scenario, 11 wetlands are still predicted to support more moorhen than we observed, which further suggests that food is not limiting moorhen numbers in Hawaii. Although in our calculations we made several assumptions about energy requirements and availability, energy amounts for 14 wetlands would have to be reduced by >98% to predict the numbers of individuals we observed during surveys. One site (Waihee) only would have to experience a 55% reduction in energy to accurately

Table 2. Total area (ha) covered by each food plant species, total gross wetland energy (TWE; GJ), and abundances of Hawaiian moorhen (M), Hawaiian coot (C), and Hawaiian duck–mallard hybrids (D) in wetlands on Oahu, Hawaii, USA. Moorhen abundance data are from DesRochers et al. (2008), and coot and duck abundances are from 2006 surveys on Oahu from the Hawaii Bi-annual Waterbird Survey database.

	Area covered by each plant species												Bird abundance		
Wetland	Pickleweed	Saltmarsh bulrush	Bermuda grass	Java sedge	Manyspike flatsedge (seeds)	Manyspike flatsedge (young shoots)	*Echinochloa* spp.	Common waterweed	California bulrush	Common cattail	California grass (<10 cm tall)	TWE	M	C	D
Kii	2.86	0.07	4.31	1.17	1.96	0.11	1.10		3.56	0.20	4.31	221.45	40	156	111
Hamakua	3.60	0.12										59.99	19	0	21
Kaelepulu	0.17	0.01										2.83	14	49	14
Turtle Bay									2.07			31.06	5	0	0
Coconut Grove	3.16								4.55			119.53	3	0	0
Hoomaluhia								10.08				214.82	3	88	0
Ukoa									35.88			537.39	3	0	0
Waihee										0.03		0.53	3	0	4
Apokaa	1.44											23.34	2	0	0
Pouhala	25.56	0.50								0.68		435.51	1	0	0
Punamano									8.40			125.77	1	1	20
Apua	0.10											1.63	0	0	5
Honouliuli	0.03	0.05								0.36		8.52	0	66	14
Salt Lake	1.15	0.98										30.83	0	19	2
Waiawa	4.60											74.80	0	3	2

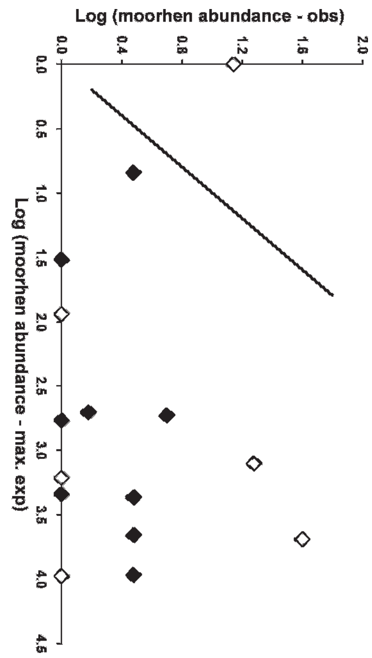

Figure 1. Number of Hawaiian moorhen we observed at Oahu, Hawaii, USA, wetlands (June–July 2006) versus maximum number of Hawaiian moorhen predicted to be supported at a wetland for 1 month if moorhen were able to metabolize a maximum amount of energy after competition with Hawaiian coots and ducks plus the energetic costs for moorhen to produce young to fledging. Coot and duck abundance data were for the same time period from Hawaii's Bi-annual Waterbird Survey database. Hollow symbols indicate wetlands managed for habitat via habitat manipulation and predator control, and solid symbols indicate unmanaged sites. The solid line represents the equilibrium between observed and predicted populations.

predict our observed moorhen numbers. The lack of correlation between abundance and food especially after controlling for wetland area suggests that either energy abundance is not a factor in wetland selection, or once a minimum amount of food is available that other factors affect population size and density. That is, we would not expect a limitation to moorhen populations unless food was much less abundant than we observed.

Even though we found no relationship between moorhen numbers and energy, many studies reported close relationships between energy and numbers of different vertebrate groups, including birds, for several spatial scales across seasons (e.g., Currie 1991, Hurlbert and Haskell 2003, Hurlbert 2004). For example, Evans et al. (2006) reported that avian species richness was positively associated with energy measures and that the relationship was stronger for wintering birds. In addition, managed playa wetlands supported greater gross energy than nonmanaged wetlands and were predicted to support higher waterfowl abundance than nonmanaged sites based on either metabolizable energy of plant seeds or invertebrates, and, in fact, the managed wetlands did support higher abundances (Anderson and Smith 1998, 1999). Furthermore, many other examples relate population numbers to food (see summaries by Newton 2003, table 7.5). Alternatively, evaluating the relationship between species abundance and food may reveal malnutrition due to an environmental problem. For example, black-necked swans (*Cygnus melanocoryphus*) experienced malnutrition despite inhabiting a priority conservation area because water pollution, in turn, caused a population decline in the swans (Artacho et al. 2007).

In addition to observed Hawaiian moorhen population sizes being below the maximum predicted, mean density of moorhen at our surveyed wetlands (2.0 birds/ha) also fell below densities of 2 Hawaiian moorhen populations reported in Nagata (1983; 17.4 in artificial wetlands and

2.5 birds/ha in a natural wetland that was restored and is managed [Hamakua], all on Oahu). We were not able to include artificial wetlands in our study but we did include the natural wetland where we observed 2.6 birds/ha. Kaelepulu supported 23.3 moorhen/ha and was the only other wetland that supported a density higher than the maximum reported by Nagata (1983). Our mean density was slightly higher than the 1.8 birds/ha reported by Chang (1990) for moorhen in an impoundment at Kii, but the density we observed at the refuge was lower (1.0 birds/ha). Also, our mean density was higher than the density calculated for Hawaiian moorhen at Hanalei National Wildlife Refuge on Kauai (0.1 moorhen/ha; Byrd and Zeillemaker 1981). Our density fell in the range reported for populations of the North American subspecies of common moorhen (*G. c. cachinnans*; 1.2–9.2 breeding birds/ha; Bannor and Kiviat 2002) but was lower than reported for the Mariana subspecies of the common moorhen (*G. c. guami*; 5.0 birds/ha) occurring in 21 ponds in Guam (Ritter and Savidge 1999).

Despite the lack of relationship between moorhen numbers and energy and protein, all wetlands except for Kaelepulu were predicted to support more moorhen under energetic constrants than were observed during call-broadcast surveys (DesRochers et al. 2008). At Kaelepulu where more moorhen were observed ($n = 14$ ad) than predicted, coots and ducks were calculated to consume more food than was available. This discrepancy probably resulted from the many coots observed loafing in vegetated areas of the wetland (D. W. DesRochers, personal observation). Typically, however, coots forage in more open areas (Pratt and Brisbin 2002).

Hawaiian moorhen also did not appear to select wetlands based on energy or protein even after controlling for wetland area. More specifically, moorhen did not appear to sort themselves based on amount of energy or protein present; we cannot rule out that moorhen require some minimum amount of either energy or protein before settling, but amounts above that minimum are not important. That not even protein seems to be related to moorhen abundance is surprising because this macronutrient is thought to limit vertebrate herbivores (Mattson 1980), and birds require more protein for key life-history events such as molt and reproduction (Murphy 1996, Klasing 2006). Furthermore, avian herbivores are generally efficient at selecting nitrogen-rich foraging areas (Lance 1983, Mills et al. 1991). Even when vegetative cover of high-nitrogen plants is low in relation to other forage species, avian herbivores preferentially forage on the high-nitrogen plants, but the extent to which moorhen are able to preferentially forage is unknown (Sedinger and Raveling 1984, Buchsbaum and Valiela 1987).

Moorhen were not present at all 15 of our surveyed wetlands despite occurrence of food resources at all sites, but moorhen occurred in sites with the lowest amount of energy and protein. It is unlikely that we missed moorhen during call-broadcast surveys due to effectiveness of playback and the small sizes of those wetlands (DesRochers et al. 2008). Thus, other factors may prevent moorhen from using those sites, such as presence of predators, absence of resources such as suitable habitat cover, or because moorhen populations are below carrying capacity on Oahu. Griffin et al. (1989) argued against the last possibility, suggesting that historical wetland area in Hawaii was limiting even before human activity began accelerating habitat loss and degradation. Although there is no direct evidence that wetland loss is limiting moorhen, loss of wetland habitat is widely viewed as a cause of waterbird decline in Hawaii, as well as globally for other members of the rail family (Shallenberger 1977, Coleman 1981, Eddleman et al. 1988, Griffin et al. 1989). Furthermore, many Hawaiian wetlands are degraded because of modified hydrologic regimes and invasive wetland plant species (U.S. Fish and Wildlife Service 2005). Dispersion of vegetation within the habitat may be particularly relevant for influencing moorhen numbers in Hawaii because it could influence how moorhen and Hawaiian coots interact. Specifically, coots are known to aggressively exclude moorhen from foraging areas, but dispersion of vegetation that creates visual barriers between adjacent territories may alleviate this competition (Murkin et al. 1982; Rehm and Baldassarre 2007; M. Silbernagle, United States Fish and Wildlife Service, personal communication). Another possible limitation to moorhen population presence and size in Hawaii is presence of predators, which pose a problem for waterbirds (U.S. Fish and Wildlife Service 2005). In fact, wetlands where moorhen are absent typically support large numbers of mammalian predators (D. W. DesRochers, personal observation). Although there is extensive anecdotal evidence of depredation of Hawaiian waterbirds by exotic predators (e.g., Coleman 1981, Stone et al. 1994), intensive studies of depredation rates and population-level effects currently are lacking.

MANAGEMENT IMPLICATIONS

It remains unclear what limits numbers of Hawaiian moorhen. We suggest that in areas that have suitable wetland vegetation for breeding, Hawaiian moorhen have sufficient food resources from an energetic standpoint even if there is one species of food plant present. However, the lack of energy or protein limitation should be further qualified because of the various assumptions that we needed to make given the limited data on this endangered species. Specifically, more information is required about the Hawaiian Moorhen's metabolism (sensu McNab 2002), ability to metabolize specific food plants, and foraging patterns because it is unlikely that moorhen eat available foods in proportion to availability.

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