TABLE 2. Food preferences of ctenosaurs given the choice between several food types. Data represents percentage of times ctenosaurs chose each food type first, second and third.

Food Type	Percent of times chosen first	Percent of times chosen second	Percent of times chosen third
Fruit	73	17.6	8.3
Meat	27	64.7	16.7
Insects	0	11.7	58.3
Flowers	0	5.9	16.7
Leaves	0	0	0

ctenosaurs consumed greater than 50% of the foods they chose in the petri dishes, except in the case of the flowers of which they consumed less than 40% ($F_{3, 49} = 7.39$, $P = 0.0004$, for test of no difference among food types in percentage consumed; Fig. 1).

Discussion

When given the choice between fruit, meat, insects, flowers and leaves, ctenosaurs prefer primarily fruit, secondarily meat and then insects, flowers and leaves respectively. Our results support the hypothesis that when given the opportunity, ctenosaurs will choose foods that we presume to have the highest nutritional value instead of choosing the leaves that generally compose most of their diet. This strategy should maximize their nutritional intake. Ctenosaurs may primarily consume low-growing vegetation because this food source is plentiful and can be obtained with less effort and skill than, for example, hunting insects or small mammals. Ctenosaurs may be opportunistic eaters who maximize their nutritional intake when they have the chance. Under normal circumstances, it is likely that they do not often expend the energy required, or have the ability, to capture live animal food.

Possible problems with our experimental design include the presentation method, as well as the types of food we offered. Because the type of cooked meat that we used would never be found in nature (except in human refuse), the presentation of an improbable food source may have affected our results. Nevertheless, a strong preference for meat was shown and this suggests a preference for highly nutritional food source. This study demonstrates that, although organisms may have a wide variety of dietary habits, their realized diet is potentially limited by food availability and the costs associated with food capture.

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Avifauna diversity and abundance in different habitats in the Tempisque River Basin, Costa Rica

Benjamin B. Risk and Kathryn M. Alexander

Abstract: Recently, the plant community composition of the Palo Verde marsh has undergone rapid transformation, from a mix of open water and floating vegetation to a community increasingly dominated by cattail. This change in habitat structure is believed to have detrimentally influenced avifauna. Resource managers propose to bulldoze and introduce cattle to 60 ha of marsh to make it more suitable for waterfowl and other wildlife. The goal of our study was to inventory the bird community in this sector of the marsh and to analyze the distribution of birds across the major habitat types. We hypothesized that bird diversity and abundance would differ across habitat types, specifically that cattail-dominated habitat would have the least bird diversity and open water mixed with floating vegetation would have the highest diversity. We found strong habitat patterns. Avian diversity was highest in sites dominated by *Thalia geniculata*. The lowest diversity was in the floating vegetation and grass-dominated habitat and cattail had low to intermediate diversity. Although cattail is associated with reduced bird diversity, the area scheduled for intensive management is composed of many other habitats containing high diversity, and the proposed habitat modification could potentially adversely affect these areas. Hopefully, this study provides a first step in continuing assessments of management affects on avian communities in the Palo Verde Marshlands.

Key Words: bird diversity, management, Palo Verde marshland

Introduction

In the past 25 years, the plant community in the marshlands of Palo Verde National Park in the Tempisque River Basin, Costa Rica, has been undergoing great change (Abram et al. 1994, McCoy and Rodríguez 1994), and great shifts in the bird community have coincided with these changes. Previously, cattle grazing maintained the less-dense vegetation habitat, thereby providing wintering habitat for blue-winged teal (*Anas discors*), American wigeon (*Anas americana*), Northern shoveler (*Anas clypeata*), and other waterfowl, as well as rare residents like the Jabiru (*Jabiru mycteria*), but since then much of the more open-water habitats have been replaced by cattail (*Typha domingenis*) and palo verde trees (*Parkinsonia aculeata*). Recent concerns over the decline in waterfowl and the changing marshland has spurred OET/OTS, the park service and Ducks Unlimited, Int., to develop a management plan for the restoration of bird diversity in this area. Under this plan, these organizations will reduce cattail cover and create more open water in these marshlands. Currently, 60 ha have been designated for intensive management. Beginning in 2002, 9 ha are scheduled to be bulldozed and then stocked with cattle to discourage the growth of cattail and palo verde. Scientific documentation of the current status of the community in the marshlands of Palo Verde is apparently lacking. The goal of this study was to inventory the bird community and the distribution of these birds across habitats at one point during the dry season (while winter-residents were present) as a baseline record of birds in this wetland. We hope that this will motivate continuing investigations of the effects of new management regimes on marshland birds.

We hypothesized that bird diversity and abundance would differ across habitats. Specifically, we predicted that bird diversity and abundance would be least in the cattails and greater in the more open habitats characterized by floating vegetation and patches of open water. Cattails were expected to have less bird diversity because the low light penetration and low palatability of cattail could

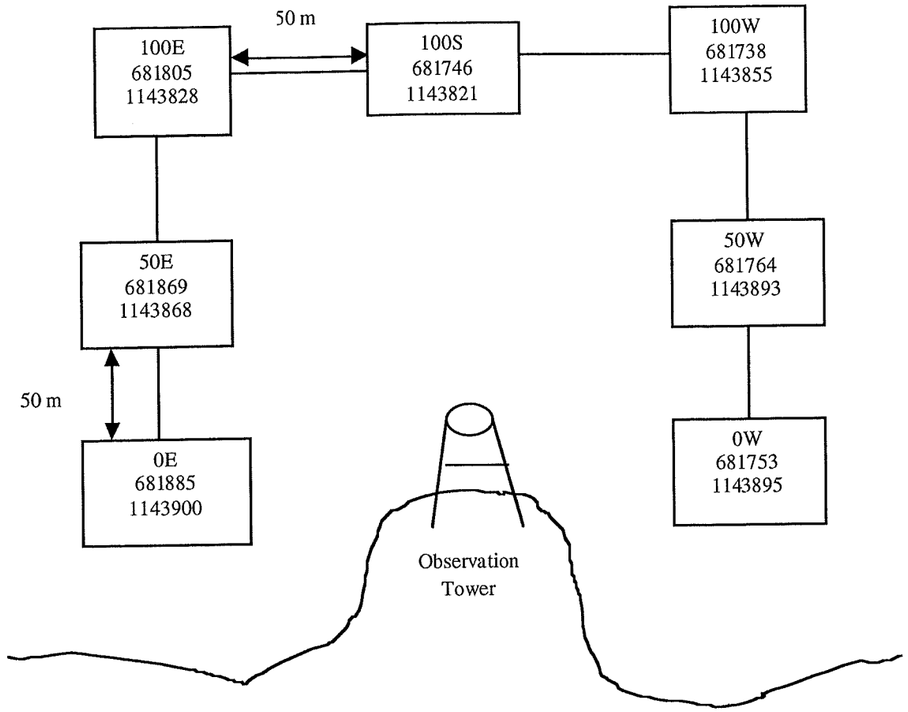

FIG. 1a. Map (not drawn to scale) and UMT coordinates for the control site in Palo Verde National Park, Costa Rica. The boxes represent the points that were sampled, not the actual area censused. Some points only accurate to within 20 m due to insufficient satellite cover.

lead to a low abundance of prey items. In the more open habitat, food may be more available, as there is a greater variety of substrate, including waterlily (*Nymphaea ampla*), mimosa (*Neptunia plena*), water hyacinth (*Eichhornia crassipes*) and water lettuce (*Pistia stratioles*). Additionally, wading birds may have easier access to fish, snails and other food items in the floating vegetation, as well as have increased mobility for foraging and increased visibility for courtship displays.

METHODS

The study was conducted on two plots in the marshland of Palo Verde National Park near the OTS Biological Station on 11 - 12 January 2002. Plot 1 was located in the marsh around the observation tower, about 300 m south of the station in an area that is not going to be manipulated in the near future (Fig. 1a). Therefore, it can serve as a control area in future studies. Plot 2 was located 300 m west of the observation tower at the west end of the airstrip, within the area designated to be bulldozed and stocked with cattle in the spring of 2002 (Fig. 1b). Both plots contained the following major habitat types as defined by dominant vegetation: (1) cattail (*Typha domingenis*), (2) sedge (*Cyperus tenerrimus*), (3) Poaceae spp., (4) floating vegetation (*Nymphaea ampla, Eichhornia crassipes, Pistia stratiotes and Neptunia plena*), (5) thalia (*Thalia geniculata*) and (6) palo verde (*Parkinsonia aculeata*).

Birds were censused at 7 randomly se-

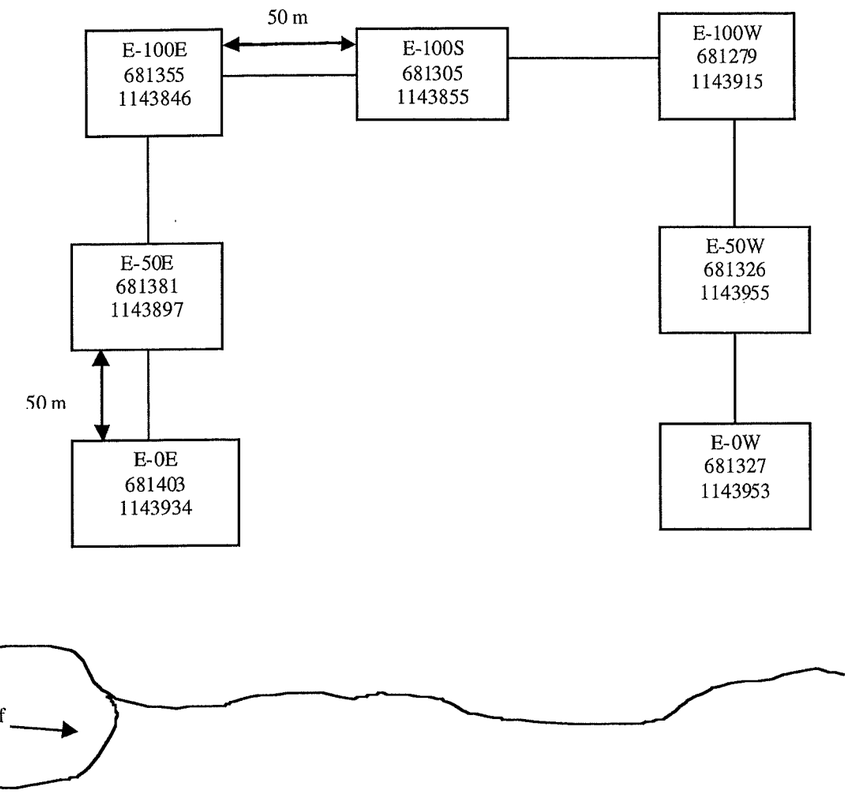

FIG. 1b. Map (not drawn to scale) and UMT coordinates for the pre-manipulation site in Palo Verde National Park, Costa Rica. The boxes are representative of points, not the actual area censused.

lected points in each 100 x 100 m plot (Fig. 1). All birds heard and observed on the way to a point were recorded, and then observations were made for 5 min at each point. We also recorded the habitat in which an individual occurred, and attempted to note whether it was previously observed. Points were censused twice, once from 07:00 - 09:00, and again from 16:00 - 17:45. At each point, we estimated relative abundance of each vegetation type within a 25 m radius. Separately, an extended area of Plot 1 was censused in sixteen 10 min observation-tower counts throughout the 2 test days.

We used t-tests to compare the amount of each habitat type in the control and pre-manipulation plot. For each plot, we calculated Simpson's diversity indices and Shannon-Weiner indices (natural logarithm) for each site (Begon et al. 1990), using the highest recorded count for each species as a measure of abundance. We did not include the birds that only flew over the sites or terrestrial birds not typically associated with the marsh, although these were recorded and are in Appendix. We also generated a rank abundance curve and calculated Simpson's diversity and Shannon-Weiner indices (natural log) (Feinsinger 2001) for all species observed (including fly-overs) in the series of counts from the lookout tower (using the highest recorded count for each species as a measure of abundance).

We calculated bird diversity indices and generated rank abundance curves for each of the 6 habitats, using the pooled data from

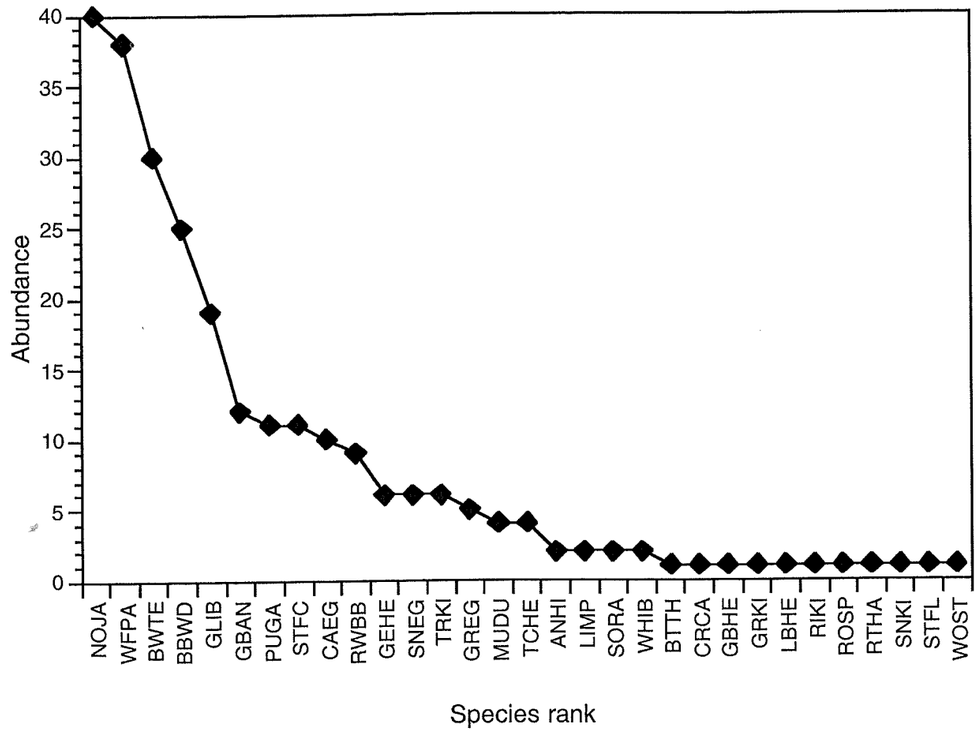

FIG. 2. Rank abundance curve for bird species recorded during 10 min point counts from the observation tower (n = 15 point counts). See Appendix for species abbreviations.

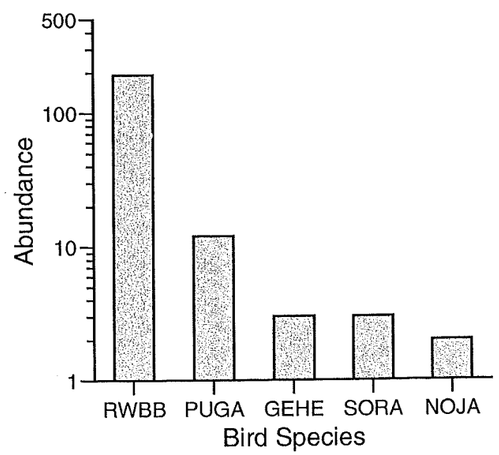

FIG. 3. Rank abundance of bird species in cattail (*Typha domingenis*) habitat during point counts in two sites of Palo Verde National Park, Costa Rica. This graph includes one sighting of 189 roosting red-winged blackbirds. (n = 213)

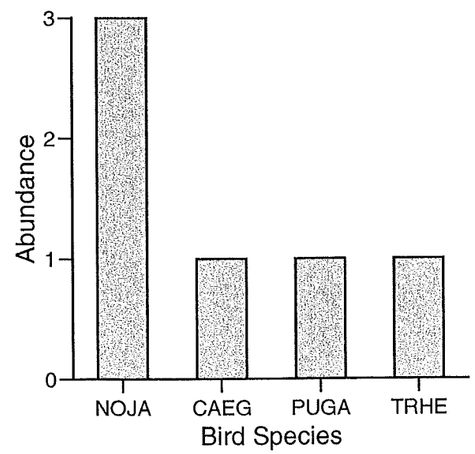

FIG. 4. Rank abundance of bird species in sedge (*Cyperus tenerrimus*) dominated habitat during point counts in two sites of Palo Verde National Park, Costa Rica. (n = 6)

the 2 sites. Abundance for each species in each habitat was calculated as the sum of all observations from 1 habitat. For individuals that were observed moving from one habitat to a nearby habitat, only the first habitat type was used. Birds that flew from one point to another (i.e., greater than 25 m) were potentially included twice in these habitat analyses, but were arguably independent for our purposes in that they represent 2 separate habitat choices.

We conducted G-tests of the number of species and the number of individuals occurring in each habitat compared to that expected based on relative proportions of each habitat present. Expected frequencies were estimated by 1) calculating the percentage of each habitat type within the total area censused, as determined by the 25 m radius visual estimate, and 2) multiplying the number of species or number of individuals observed over all the habitats by this number.

Results

We observed a total of 39 species in the two sites combined (Appendix), with high counts for each species summing to 288 individuals from 14 species in the control area and 102 individuals from 23 species in the pre-manipulation area. Diversity measures (Simpson's D and Shannon-Weiner's H) were somewhat higher in the pre-manipulation plot than in the control ($D_{control} = 1.92$, $D_{pre\text{-}manipulation} = 2.78$; $H_{control} = 1.14$, $H_{premanipulatin} = 1.84$). We recorded 31 bird species from the tower (Fig. 2): Simpson's Diversity = 11.43 and Shannon-Weiner = 2.77.

The amount of each vegetation type varied from 2.1% for palo verde to 25.0% for floating vegetation, but, except for palo verde, the amounts of habitat in the two plots were similar (Table 1). Rank abundance curves revealed strong differences in the bird communities associated with different vegetation types (Fig. 3 - 9). We found only 5 species and 213 individuals in the cattail (189 individuals were one flock of red-winged blackbirds, *Agelaius phoeniceus*, that flew into the cattail during one count; Fig. 3). The Cyperaceae also had a low number of species, with only 6 individuals of 4 species (Fig. 4). The floating vegetation had 7 species, but was dominated by Northern Jaçana (Fig. 5). Palo verde had a relatively large number of species but relatively few birds of any one species (Fig. 6), while the grass-dominated habitat had a similar number of species, but had large numbers of Northern jaçana (Fig. 7). We found the most species in thalia, 12 species represented by 106 individuals, that were quite evenly distributed (Fig. 8). Both the Simpson and Shannon-Weiner diversity index indicated the following heirarchy in diversity, listed from least to greatest: floating, Poaceae, Cyperaceae, cattail, palo verde, thalia (Table 2). If outlying data from a roosting flock of red-wing blackbirds is included, the heirarchy is: floating, cattail, Poaceae, Cyperaceae, palo verde and thalia.

When controlling for differences in the

TABLE 1. Percentage of six habitat types (mean ± SE) in the control plot compared to the premanipulation plot (t-tests compare plots; df = 12).

Habitat Type	Control	Premanipulation	t-value	p-value
cattail	21.43 ± 12.18	7.86 ± 4.21	1.05	0.31
cyperaceae	17.14 ± 8.51	20.00 ± 6.90	0.26	0.8
poaceae	22.14 ± 9.11	25.71 ± 11.15	0.25	0.81
floating	20.71 ± 10.03	29.29 ± 10.82	0.58	0.57
thalia	14.29 ± 4.81	17.14 ± 10.23	0.25	0.8
palo verde	4.29 ± 1.70	0.00 ± 0.00	2.52	0.03

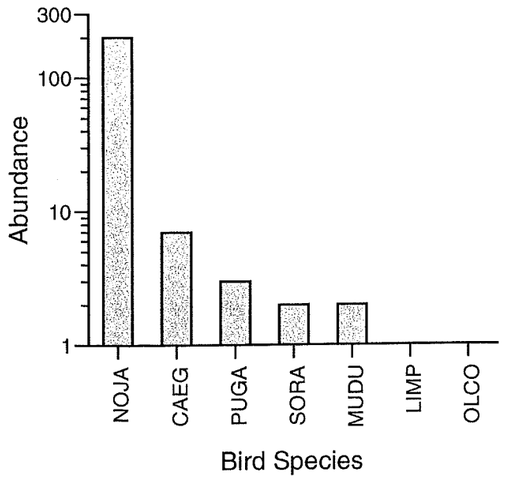

FIG. 5. Rank abundance of bird species in floating vegetation, primarily consisting of *Nymphaea ampla, Eichhornia crassipes, Pistia stratiotes* and *Neptunia plena,* with occasional grass, sedge and open water, during point counts at 2 sites in Palo Verde National Park, Costa Rica (n = 217).

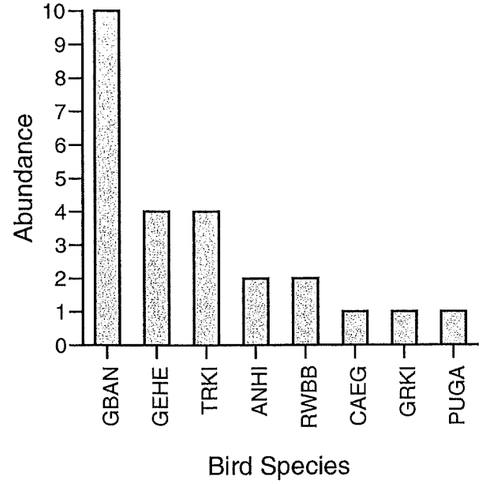

FIG. 6. Rank abundance of bird species found in palo verde trees during point counts in two sites of Palo Verde National Park, Costa Rica. (n = 25)

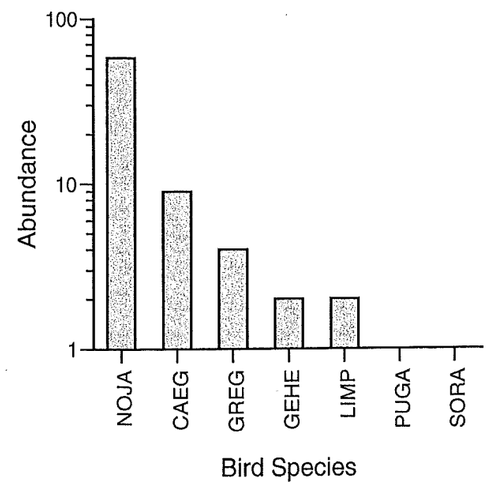

FIG. 7. Rank abundance of bird species in grass-dominated habitat during point counts in two sites of Palo Verde National Park, Costa Rica (n = 77).

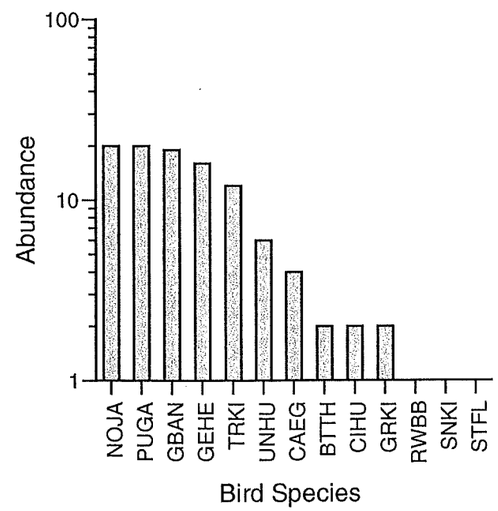

FIG. 8. Rank abundance of bird species in thalia (*Thalia geniculata*) during point counts in two sites of Palo Verde National Park, Costa Rica. (n = 106)

amount of each habitat censused, there were still large differences in number of species (χ^2 = 30.36, df = 5, P < 0.001; Fig. 9) and individuals (Likelihood-ratio χ^2 = 408.80, df = 5, P << 0.001; Fig. 10) across habitats. Cattails, Cyperaceae and Poaceae had fewer individuals of fewer bird species than expected based on the amount of habitat (Fig. 9 - 10). Palo verde had far higher species richness than expected (Fig. 9). Floating and thalia habitats held more bird individuals than expected based on area (Fig. 10).

TABLE 2. Diversity indices for birds in six habitat types at Palo Verde National Park, Costa Rica. Data were pooled from the two study plots. Cattail indices are with a roost of 189 red-winged blackbirds (first value)and without (second value).

Habitat Type	% of study area (mean ± SE)	Shannon-Weiner diversity	Simpson's diversity
cattail	14.6 ± 6.7	0.41; 1.37	1.21; 3.16
cyperaceae	18.6 ± 5.3	1.24	3
poaceae	23.9 ± 6.9	0.92	1.71
floating	25.0 ± 7.2	0.38	1.16
thalia	15.7 ± 5.4	2.11	6.9
palo verde	2.1 ± 1.0	1.74	4.37

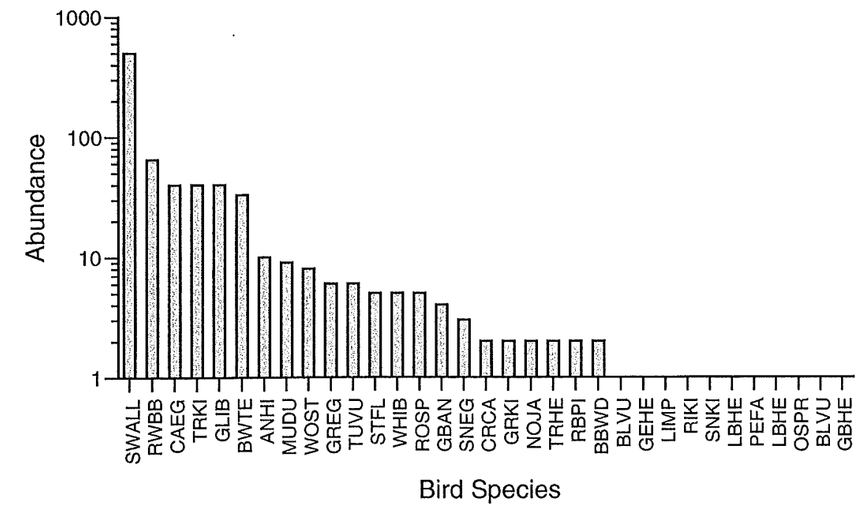

FIG. 9. Rank abundance of bird species seen flying over two observers during point counts in two sites of Palo Verde National Park, Costa Rica. This graph includes one sigthing of 500 swallows flying from the woods to forage over the marsh (n = 802).

Discussion

The control plot and pre-manipulation plot were very similar in their vegetation structure and reasonably similar in avian diversity (Table 1). Our judgment is that increased sampling time would bring the diversity indices closer to each other and produce rank abundance patterns for both plots that resemble our tower data (Fig. 2). This baseline similarity between the plots makes them appropriate for assessing changes in bird communities due to the planned landscape manipulations.

Bird diversity varied greatly across habitats, supporting the hypothesis that different habitats support different abundance and diversity of birds. Our prediction that cattail would support less diversity than other habitats was partly supported (Table 2), but whether it had low or moderate diversity depends on how the roost of red-winged blackbirds was treated. Red-winged blackbirds regularly roost within cattails during night, but forage throughout the marsh during the day. Bird observations could have been bi-

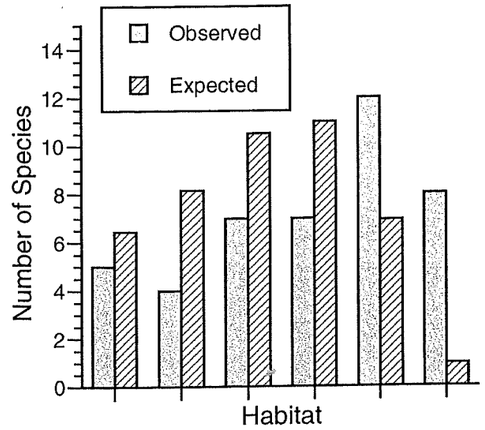

FIG. 10. Number of bird species in each habitat type compared to number expected based on amount of habitat.

ased downwards in cattails because visibility in cattails is lower than other habitats. However, we doubt that this bias was substantive because observations were also based on bird calls, and when we walked through thick stands of cattails we failed to find or flush any birds (as further confirmed by an observer in the lookout tower over Site 1).

A use of the cattails not well captured by our experimental protocol is the propensity for many birds to aggregate near the edge of cattail, perhaps because of the refuge the birds are afforded in the event of a fly-by predator. Additionally, species such as sora (*Porzana carolina*) and purple gallinule (*Porphyrula martinica*) were observed moving in and out of the cattail, possibly using the cattail for cover while coming out to feed in other vegetation. Our study plots did not include extensive monospecific stands of cattails, and nearly all birds observed in cattail were near the edge of cattail patches in close proximity to other habitats. It seems likely that large cattail patches support even less avian diversity than our study indicates. However, cattail patches of 10 - 20 m^2, such as occurred in our sample plots, probably benefit numerous bird species that exploit cattails for shelter and roosting. Thus, small stands of cattail are not obviously detrimental to species diversity, and perhaps are important as a place for shelter.

We also found that the sedge-dominated habitat had low diversity and extremely low numbers of individuals (Fig. 4, 10, 11). This habitat was generally avoided by the birds, although the reasons were not apparent. Hypothesized causes for the decline in bird diversity in the Palo Verde marshland have not included a role for *Cyperus tenerrimus*, but future studies should investigate whether the abundance of this sedge is

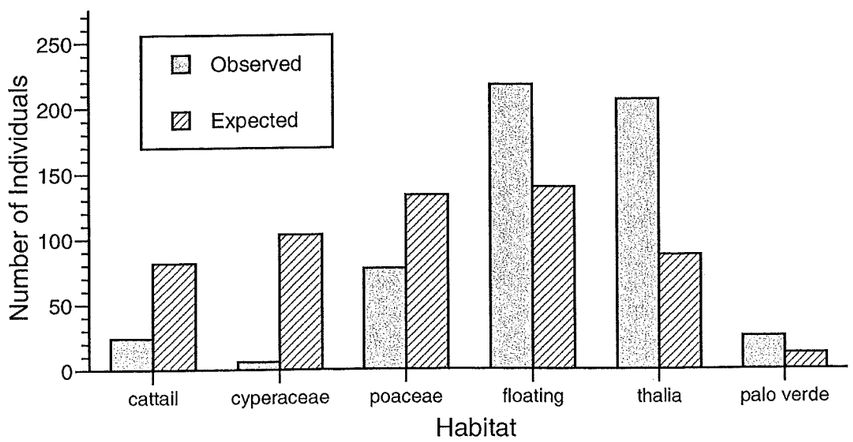

FIG. 11. Sum of individuals observed in each habitat and number of individuals expected given amount of habitat.

changing, and assess its direct impacts on bird diversity.

Contrary to our expectations, floating vegetation had the lowest diversity indices (Table 2), and far fewer species than expected based on area (Fig. 10). However, this vegetation type did have a larger representation of total individuals than expected, mostly due to Northern jaçanas (Fig. 11). Furthermore, this was the only habitat in which muscovy duck and olivaceous cormorant were found, and one of just two habitats with limpkin (Fig. 3). Thus, the floating vegetation has low alpha diversity but contributes to the overall beta diversity of the plot.

Surprisingly, thalia-dominated habitat contained the most bird species and individuals relative to its area (Fig. 10, 11). Thalia was in bloom during our study, and purple gallinules and other birds were feeding on the flowers and/or seeds. Thalia is important to bird diversity, at least during the time of year of this census. Palo verde-dominated habitat also had high diversity, but the birds found in it were mostly not restricted to the marsh habitat (red-winged blackbirds, groove-billed ani, tropical kingbirds, great kiskadee). Mainly, the palo verde played a functional role as a perching post for territorial or fly-catching birds. Small amounts of palo verde increased overall bird diversity by adding these terrestrial species, but increases beyond this amount will result in a trade-off with the non-terrestrial species.

One problem with our protocol was that the vegetation estimates were based on a 25 m radius around the point, while the bird abundance from each point was based on total number of visible birds. Thus, the bird observations were made over an area that did not correspond precisely to the estimates of the amount of habitat censused. We doubt that this compromised the broad patterns indicated by our data.

Management Implications

Our results generally support the prevailing view of park managers that cattail does not contribute new species or great numbers of individuals to the avifaunal community. Thus, replacement of other marsh habitats by cattail seems detrimental to bird diversity. Nonetheless, small stands of cattail probably contribute to bird diversity by providing protection and nesting habitat for purple gallinule, green-backed heron, sora and red-winged blackbird.

A central management goal is to increase the amount of open water. Our results did not evaluate diversity in open water, but there is likely a tradeoff between creating open water and destroying the thalia and other critical foraging and nesting habitat. Management plans for the marshlands of Palo Verde National Park will allow some vegetation to grow in, and cattle are projected to prevent cattail from displacing other vegetation types. However, cattle grazing could create a matrix consisting mostly of grass-dominated habitat, open water and floating vegetation (Fig. 4, 5, 7). Open water may provide habitat for some species not observed in the point counts, such as black-bellied whistling ducks and blue-winged teal, but seems unlikely to provide breeding habitat. Thus, a management plan that does not allow for the growth of tall vegetation, such as thalia, will probably not maximize bird diversity. The precise effects of cattle grazing on the plant community need to be closely monitored.

An extensive area of continuous cattail that lies roughly 500 m east of the control site seems like a better candidate for manipulation than the area censused in this study. We encourage park managers to monitor effects of initial manipulations carefully, and retain the flexibility to modify plans as the program progresses.

ACKNOWLEDGEMENTS

We'd like to thank Dr. Richard T. Holmes for collecting the tower count data and aiding us in other aspects of the data collection, and for his valuable suggestions.

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APPENDIX. Abbreviations, species and resident status of birds found in and flying over the marshlands of Palo Verde. (Year-round (Y) or winter (W) resident[a])

Abbreviation	Name	Y/W
ANHI	Anhinga	Y
BBWD	Black-bellied whistling duck	Y and W
BLVU	Black vulture	Y
BTTH	Bare-throated tiger-heron	Y
BWTE	Blue-winged teal	W
CAEG	Cattle egret	Y
CIHU	Cinnamon hummingbird	Y
COYT	Common yellowthroat	W
CRCA	Crested caracara	Y
GBAN	Groove-billed ani	Y
GBHE	Great blue heron	W and Y
GEHE	Green-backed heron	Y and W
GLIB	Glossy ibis	Y and W
GREG	Great egret	Y and W
GRKI	Great kiskadee	Y
LBHE	Little blue heron	W
LIMP	Limpkin	Y
MUDU	Muscovy duck	Y

Abbreviation	Name	Y/W
NOJA	Northern jaçana	Y
OLCO	Olivaceous comorant	Y
OSPR	Osprey	W
PEFA	Peregrine falcon	W
PUGA	Purple gallinule	Y
RBPI	Red-billed pigeon	Y
RIKI	Ringed kingfisher	Y
ROSP	Roseate spoonbill	Y
RUTH	Ruby-throated humminbird[c]	W
RWBB	Red-winged blackbird	Y
SBOR	Streaked-backed oriole	Y
SNEG	Snowy egret	W and Y
SNKI	Snail kite	Y
SORA	Sora	W
STFL	Scissor-tailed flycatcher	W
SWALL	Swallows[b]	
TRHE	Tricolored heron	W
TRKI	Tropical kingbird	Y
TUVU	Turkey vulture	Y and W
UNHU	Unknown hummingbird[c]	
WCSE	White-collared seedeater	Y
WHIB	White ibis	Y
WOST	Wood stork	Y

[a]After Stiles and Skutch (1989); more common status listed first.

[b]One sighting of hundreds of swallows containing mangrove swallows, barn swallows, Southern rough-winged swallows and Northern rough-winged swallows.

[c]UNHU may have been RUTH, but we were unable to confirm species ID. Only UNHU was used in species diversity indices, as UNHU and RUTH likely represent just 1 species.