magnitude. The large black ants are regularly found foraging alone in open sandy areas, ranging widely from their nests. They can minimize losses to antlions only by individual vigilance or adept escape behavior. Their size appears to contribute to escape success, but other factors not examined in this experiment must account for the 30-fold escape advantage the large field ants held over army ants. The particular species of army ants I collected forage in tight columns of mixed soldiers and workers. Since the column works as a unit, workers probably never encounter an antlion pit alone, and do not need solo strategies for pit escape. The column would collapse a pit faster than the antlion could rebuild it, and prevent captures. Their size is probably adapted to the large prey they commonly subdue rather than predator avoidance, based on their relatively low escape rates.

Even though the small black field ants' habitat overlaps that of antlions, they were never able to escape from the traps. The species would suffer heavy losses to the antlions if they had no way of avoiding the pits. In the field, I observed these ants avoiding pits near their nest, indicating that they can detect the trap before entering it. Since my experiment placed them directly in the pit, any behavioral avoidance would have been ineffective.

My experiments showed that size reduces capture by antlions. To escape from the traps, it seems that ants must be above some minimum length. Smaller species likely employ strategies focusing not on escape, but on detection and avoidance of pits. Future studies could address behavioral mechanisms, chemical signals, tactile pit detection, and possibly sand-adapted leg morphologies which might contribute to escape or avoidance of antlion pits.

Literature Cited

Butcher, J. L., E. B. Close, and M. E. Harrison. 2002. Ant avoidance and escape from antlion pit traps. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

McClure, M. S. 1983. *Myrmeleon* (Antlions). *in* D. H. Janzen, ed. Costa Rican Natural History. University of Chicago Press: Chicago, IL. Pp. 742-743.

Effects of wetland habitat restoration on the species diversity and abundance of tropical avifuana

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Abstract: The establishment of Palo Verde National Park led to the elimination of cattle grazing from the Tempisque River basin marsh. A subsequent decrease in abundance of marsh birds was attributed to the invasion and dominance of cattails (*Typha dominguensis*). In 2002, a management effort was initiated that involved mechanically crushing areas of cattails to provide more open habitat suitable for waterfowl. We compared avian abundance and diversity before and after this recent management strategy. Bird species richness remained the same, but abundance increased following cattail crushing. Species diversity indices indicated a shift in community composition, related largely to a notable increase in the abundance of one species, the Black-bellied Whistling Duck. These results suggest that the conservation plan to restore open habitat and increase waterbird abundance is beginning to show positive results.

Key Words: marsh conservation, Typha dominguensis, *waterfowl*

Introduction

A major goal of wetland restoration is to increase species abundance and diversity through the regeneration of degraded habitat. Palo Verde National Park, in association with the Organization for Tropical Studies and Ducks Unlimited, Int., have initiated a management plan to increase waterfowl diversity in the marsh at Palo Verde, Guanacaste Province, Costa Rica. Cattle grazing was eliminated from the marsh after the creation of Palo Verde National Park in 1981, resulting in the invasion of cattails (*Typha dominguensis*) across a 500-ha expanse in subsequent years (E. Gonzalez, pers. comm.). A drop in avian abundance followed this change in the marsh habitat (R. T. Holmes, unpubl. data). This decline fueled interest in clearing cattails to restore the wetland to its earlier state, which had apparently been maintained by the trampling and grazing of cattle. Earlier attempts to clear the marsh had included burning the cattails, disking, grazing, and mowing. These methods were impractical for long term maintenance of the area, but they did create enough open water habitat to facilitate a substantial increase in bird abundance (McCoy and Rodriguez 1994).

By early January 2002, the Palo Verde marsh contained little open water and cattails dominated the landscape. To break up the cattail monoculture, it was proposed to have tractors crush down the cattails and to allow light cattle grazing to maintain open water habitat. This procedure was initiated in selected areas of the marsh.

The purpose of this study was to examine the effects of this management regime on avian abundance and diversity one year after it began. To this end, we compared species abundance and diversity in sites one year (site 1) and five months (site 2) after manipulation. Risk and Alexander (2002) conducted a census of avian abundance and diversity in January 2002, just before the first clearing, providing baseline data for our study. We hypothesized that avian species abundance and diversity would be influenced by mechanized habitat manipulation of the marsh. Specifically, we predicted that bird abundance and diversity would increase since last year as more open water, floating vegetation, and sedge habitats replaced the dense cattail cover.

Methods

We determined percentage vegetation cover and censused avian abundance for two sites in the Palo Verde marsh on 13 - 14 January 2003. Data collection and analysis were similar to those of Risk and Alexander (2002). The study area was a tropical, freshwater marsh 5 km long and 1 km wide located between the OTS field station and the Rio Tempisque (McCoy and Rodriguez 1994). Site 1 (100 x 100 m) was located ~300 m south of the OTS Biological Station, around the observation tower, and had been manipulated in January 2002. Site 2 (100 x 100 m) was located adjacent to the west end of the airstrip and had been manipulated in August 2002.

The proportion of each microhabitat type was estimated in both sites to quantify the change caused by mechanized disturbance. We used GPS coordinates to relocate the seven points used by Risk and Alexander (2002). Then, two observers visited each point and estimated percent vegetation or open water area within a 25 m radius. The microhabitat types were placed into seven categories: sedge (*Oxycaryum cubense*), grasses (Poaceae), floating vegetation (*Pistia stratioles, Eichhornia crassipes, Nymphaea ampla*), thalia (*Thalia geniculata*), palo verde (*Parkinsonia aculeata*), cattails (*Typha dominguensis*) and open water.

We recorded bird abundance using scan sampling from a vantage point above each site. At site 1, we recorded data from the observation tower, and, at site 2, we censused from a tree 7 m above the marsh near the west end of the airstrip. We conducted fifteen 10 min censuses at each site from 06:00 – 09:00 and from 16:00 – 17:45, counting numbers of birds of each species within each site for each census. Additionally, we noted the microhabitat in which each bird was observed. The final abundance of each species in a site was counted as the maximum number of individuals of that species observed in any census period. We did not include birds flying over the site and terrestrial species not regularly associated with the marsh habitat.

We altered our survey methods from those used by Risk and Alexander (2002) by recording only species abundance from a central observation point. The previous study recorded species abundance from both a central observation point and from seven specified points on the perimeter of each site. The latter method was unnecessary in 2003, because cattails that had previously obstructed the view of those points in the marsh had been crushed. We found that birds were visible throughout the area from the central observation points.

We determined whether percentages of microhabitat types differed significantly between sites 1 and 2 and overall between 2002 and 2003, using t-tests. When a particular microhabitat type was absent, a parametric t-test could not be used, so a non-parametric Wilcoxon signed-rank test was substituted. We also calculated the Shannon-Weiner and Simpson's diversity indices for bird species in each microhabitat type and for bird species in each site. These indices account for variations in species richness and abundance of each species and are sensitive to differences in relative abundance across species. Thus, communities with a high degree of species richness and evenness of abundance across species have high diversity (Begon et al. 1990). We compared our findings with those calculated by Risk and Alexander from data collected in 2002.

Results

Vegetative cover in both sites changed between 2002 and 2003. Mechanized manipulation changed the relative abundance of vegetation and open water area within each site (Table 1). In site 1, the dominant microhabitats shifted from approximately equal ratios of sedge, grasses, floating vegetation, thalia, and cattail to primarily sedge and floating vegetation. In site 2, sedge, floating vegetation, and thalia

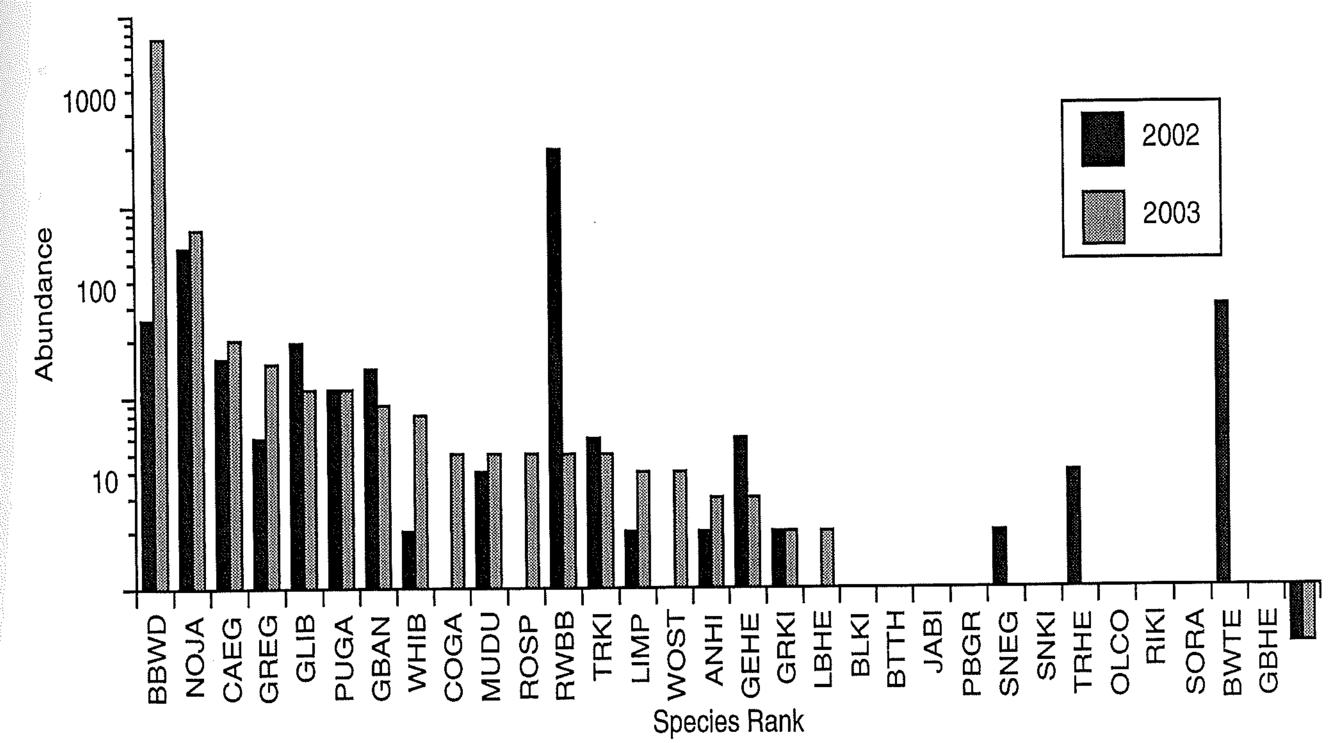

FIG 1. Rank abundance curve for bird species in two study sites in the Palo Verde Marsh in 2002 and 2003. 2002 values were pooled from 16 point counts at the observation tower and ground sightings (Risk and Alexander, 2002). 2003 values were pooled from all point counts at both sites.

became the most abundant habitats. In both sites combined, sedge was most abundant, followed by floating vegetation, cattail, open water, thalia, palo verde, and grasses.

In our censuses, we recorded 26 bird species across both sites, with maximum counts of 906 individuals in site 1 and 138 individuals in site 2 (Table 2). The dominant species in the marsh changed, as a maximum count of 750 Black-bellied Whistling Ducks replaced last year's high of 65 Northern Jacanas and a flock of 198 Red-winged Blackbirds. While the total number of species decreased by one, bird abundance was substantially higher this year. Maximum counts for both years pooled from both sites are depicted in Figure 1, organized by abundance ranking from the 2003 data. Species observed this year but not in 2002 were the Jabiru, Pied-billed Grebe, and Common Gallinule. In 2003, we did not record the Olivaceous Cormorant, Ringed Kingfisher, Sora, Great Blue Heron, or the Blue-winged Teal. The increase in bird abundance was mostly due to wading birds such as the Black-bellied Whistling Duck, Northern Jacana, Cattle Egret, Great Egret, White Ibis, Roseate Spoonbill, and Wood Stork. Notable decreases in abundance were noted for Red-winged Blackbird and the absence of Blue-winged Teal.

Bird diversity calculated using Shannon-Weiner and Simpson's diversity indices appeared to be associated with vegetative cover. Bird diversity was highest in thalia, followed by sedge, cattail, palo verde, floating vegetation, open water, and grasses (Table 3). Floating vegetation, however, contained the highest species richness with 14 distinct species, followed by thalia with 12, sedges with 11, and cattails with 5. Diversity in site 1 decreased slightly, and diversity increased markedly in site 2 (Table 3). When Black-bellied Whistling Ducks were excluded from 2003 data, diversity in both sites increased.

TABLE 1. Percentage of seven marsh microhabitat types (mean ± SE) in study sites 1 and 2 (n = 7) and both sites combined compared across years 2002 and 2003. An asterisk indicates a significant change between years ($P < 0.05$).

Habitat	Site 1		Site 2		Combined	
Type	2002[1]	2003	2002[1]	2003	2002[1]	2003
Sedge	17.1 ± 8.5	25.7 ± 8.8	20.0 ± 6.9	57.1 ± 7.1*	18.6 ± 5.3	41.4 ± 6.9*
Grasses	22.1 ± 9.1	0 ± 0*	25.7 ± 11.2	0.0 ± 0.0*	23.9 ± 6.9	0.0 ± 0.0*
Floating	20.7 ± 10.0	52.9 ± 10.1*	29.3 ± 10.8	17.1 ± 4.6*	25.0 ± 7.2	35.0 ± 7.3
Thalia	14.3 ± 4.8	0 ± 0*	17.1 ± 10.2	11.4 ± 5.1	15.7 ± 5.4	5.7 ± 2.9*
Palo Verde	4.3 ± 1.7	3.6 ± 1.8	0.0 ± 0.0	0.0 ± 0.0	2.1 ± 1.0	1.8 ± 1.0
open water	0.0 ± 0.0	10.0 ± 8.5	0.0 ± 0.0	5.7 ± 3.9	0.0 ± 0.0	7.9 ± 4.5
Cattail	21.4 ± 12.2	7.9 ± 4.3*	17.9 ± 4.2	8.6 ± 4.0	14.6 ± 6.7	8.2 ± 2.9*

[1]Risk & Alexander, 2002.

TABLE 2. Summary of bird species richness, most abundant species, total abundance, and bird diversity for the two study sites in January 2002 and January 2003. Numbers in parentheses indicate values calculated without Black-Bellied Whistling Ducks.

	Site 1		Site 2	
	2002[1]	2003	2002[1]	2003
Species richness	26	25	16	25
Most abundant species	RWBB	BBWD	NOJA	NOJA
	NOJA	NOJA	CAEG	BBWD
	BWTE	CAEG	PUGA	CAEG
	BBWD	GREG	GBAN	GLIB
	GLIB	GLIB	TRKI	PUGA
Total abundance	376	906	94	138
Shannon-Weiner DI	1.15	0.79 (2.20)	1.53	2.15 (2.03)
Simpson's DI	3.26	1.44 (4.53)	1.84	5.31 (4.39)

[1]Risk & Alexander, 2002.

TABLE 3. Diversity indices of bird species within seven microhabitat types in two years in Palo Verde National Park, Costa Rica. Calculations include data pooled from both sites.

Habitat Type	Shannon-Weiner diversity		Simpson's diversity		Bird species richness	
	2002[1]	2003	2002[1]	2003	2002[1]	2003
sedge	1.24	1.81	3.00	4.24	4	11
grasses	0.92	0.00	1.71	0.00	5	0
floating	0.38	0.62	1.16	1.33	7	14
thalia	2.11	2.21	6.90	7.28	12	12
palo verde	1.74	0.64	4.37	1.80	8	2
open water	0.00	0.00	0.00	1.00	0	1
cattail	0.41	1.41	1.21	3.66	5	5

[1]Risk & Alexander, 2002.

DISCUSSION

Bird abundance increased significantly between 2002 and 2003, owing mostly to the presence of large numbers of Black-bellied Whistling Ducks, which increased from 25 to 750 individuals, and the increase in bird abundance of wading birds that could take advantage of the open water, floating vegetation, and sedge. The absence of the Blue-winged Teal, Olivaceous Cormorant, Ringed Kingfisher, Sora, and Great Blue Heron from 2003 censuses may be due to the low detection probability of these mobile species. Their absence should not be considered evidence that they are no longer using the marsh. In fact, all of these species except the Sora were spotted during the week of our study but not during our observation periods.

While changes in abundance of certain species over time are the most important indicator of how habitat manipulation influences the avian community, changes in species richness and evenness reveal additional information about the marsh. Despite the significant increase in total bird abundance, species richness remained very similar, from 27 species in 2002 and 26 in 2003, suggesting that habitat manipulation did not compromise the number of species utilizing the marsh. We found a small decrease in bird diversity at site 1, using indices combining species richness and evenness. The decrease was due in large part to the high numbers of Black-bellied Whistling Ducks, which greatly decreased evenness in the community. Diversity increased in site 2, because species richness was higher, while evenness did not change.

Our data suggests that marsh vegetative cover influences changes in avian community structure. We found that increases in bird diversity indices corresponded with increases in sedge and floating vegetation. These microhabitats also contained the greatest number of individuals, supporting our prediction. However, decreases in thalia and cattail were correlated with increases in bird diversity. While this latter pattern is contrary to our hypothesis, it may be explained by the edge effect created by these emergent plants. Since most bird species found in thalia and cattail (Purple Gallinule, Cattle Egret, Groove-billed Ani, Common Gallinule, Red-winged Blackbird) inhabited the edge, we speculate that the reduction in area of these vegetation types does not decrease their utility as edge microhabitats unless they are completely eradicated. Therefore, a decrease in abundance of these microhabitats might not have much effect on bird diversity.

While changes in species diversity are usually measured over longer periods of time than the duration of our study, our observations provided an evaluation of the effect of large-scale habitat disturbance on avian diversity and abundance after five months and one year. Our research represents the second year in an ongoing study of avian populations at the Palo Verde marsh and the first data collected since habitat manipulation began. Our study suggests that the management plan has been successful in altering the marsh habitat by crushing stands of cattail and thalia in order to encourage the growth of sedges, water hyacinth, water lettuce, and water lily and provide more open water. Furthermore, this success in curtailing the growth of cattails in the marsh has encouraged the return of water birds to this part of the marsh, especially those that can utilize the open water and floating vegetation for resting and foraging. Continued management of cattails may restore avian abundance to pre-1981 levels. We encourage future studies to monitor changes in the bird assemblage in the marsh as the park continues to alter the habitat.

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LITERATURE CITED

Begon, M., J. L. Harper, and C. R. Townsend. 1990 *Ecology: Individuals, Populations and Communities.* 2nd Ed. Blackwell Scientific Publications: Boston, MA.

McCoy, M. B. and J. M. Rodriguez. 1994. Cattail (*Typha dominguensis*) eradication methods in the restoration of a tropical, seasonal, freshwater marsh. *in* W. J. Mitsch, ed. Global Wetlands: Old World and New. Elsevier Science. Pp. 469-482.

Risk, B. B. and K. M. Alexander. 2002. Avifauna diversity and abundance in different habitats in the Tempisque River Basin, Costa Rica. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

APPENDIX 1. Symbols and corresponding common names of birds observed in the marsh at Palo Verde in 2002 and 2003.

Symbol	Common Name	Symbol	Common Name
ANHI	Anhinga	MUDU	Muscovy Duck
BLKI	Belted Kingfisher	NOJA	Northern Jacana
BBWD	Black-bellied Whistling Duck	OLCO	Olivaceous Cormorant
BTTH	Bare-throated Tiger Heron	PBGR	Pied-billed Grebe
BWTE	Blue-winged Teal	PUGA	Purple Gallinule
CAEG	Cattle Egret	ROSP	Roseate Spoonbill
COGA	Common Gallinule	RIKI	Ringed Kingfisher
GBAN	Groove-billed Ani	RWBB	Red-winged Blackbird
GBHE	Great Blue Heron	SNEG	Snowy Egret
GEHE	Green-backed Heron	SNKI	Snail Kite
GLIB	Glossy Ibis	SORA	Sora
GREG	Great Egret	TCHE	Tri-colored Heron
GRKI	Great Kiskadee	TRKI	Tropical Kingbird
JABI	Jabiru	WHIB	White Ibis
LBHE	Little Blue Heron	WOST	Wood Stork
LIMP	Limpkin		