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BIRDS ARE OVERLOOKED TOP PREDATORS IN AQUATIC FOOD WEBS

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Abstract. Most freshwater food web models assume that fish occupy the top trophic level. Yet many diet studies and a few caging and artificial stream experiments suggest that birds may be top predators in many freshwater systems. We conducted a large-scale field experiment to test whether avian predators affect the size distribution and abundance of fish in two midwestern streams. We used a combination of netting and perches to manipulate predation by Great Blue Herons (*Ardea herodias*) and Belted Kingfishers (*Ceryle alcyon*), and measured the response in the fish assemblage. Bird exclusions caused significant increases in medium size classes of two common prey, striped shiners (*Luxilus chrysocephalus*) and central stonerollers (*Campostoma anomalum*). We show that these species of piscivorous birds can alter the abundance of common prey and thus need to be considered more fully when attempting to explain the structure of aquatic food webs.

Key words: *Ardea*; birds; riparian; *Campostoma*; *Ceryle*; cyprinid; fish; food webs, aquatic; heron; kingfisher; *Luxilus*; predator; prey; shiner; stoneroller.

INTRODUCTION

Knowing which species are strong interactors in a food web is fundamentally necessary to understanding its dynamics (Power et al. 1995, Wootton 1997). Conventional models of freshwater food webs assume that fish occupy the top trophic level and are the most important biotic determinant of trophic abundance lower down in the food web (Vannote et al. 1980, Fry 1991, Wellborn et al. 1996). However, many terrestrial predators, including many bird species, feed on aquatic systems, and therefore are components of trophic levels in aquatic food webs. They thus have the potential to be important drivers of aquatic food web dynamics.

For example, when grazing catfish were placed in cages of various depths, fish disappeared from shallow cages, but survived in deeper cages where avian predators were ineffective foragers (Power et al. 1989). The predation risk in the shallow water of these streams was so strong that catfish would not feed on visible bands of algae along stream margins, even when resources in deeper parts were scarce (Power 1984). Tank and artificial stream experiments have shown similar

changes in foraging behavior, habitat use, and growth rates (Milinski and Heller 1978, Harvey and Stewart 1991, Allouche and Gaudin 2001). These studies suggest that avian predators may impose both lethal and nonlethal impacts on fish populations.

Understanding the function of these potential top predators also has important management implications. There is a recurring concern among fisheries managers that avian predators may impact game fish populations (reviewed in Draulans 1988). This concern has intensified in recent years as populations of many fish-eating bird species have expanded in size and range (Feltham 1995, van Eerden et al. 1995, Glahn et al. 1998). Most studies examining the issue of bird impacts have been diet studies of piscivorous birds linked with fish population estimates in hatcheries, reservoirs, or stocked populations (Draulans 1988). However, diet studies by themselves are insufficient to provide critical understanding of predator effects on dynamics.

The key step in determining the importance of avian predators in aquatic systems is to know whether they can alter the abundance or behavior of any of their prey species. Here we report the results of a large-scale field experiment designed to examine whether avian predators can significantly affect fish populations in streams.

METHODS

The study was conducted at Midewin National Tallgrass Prairie, Illinois, USA. Two streams, Prairie Creek

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and Jackson Creek, were used for the study. Both streams are stony-bottomed, low-gradient, third-order streams fed principally by surface runoff, shallow groundwater, and field tile discharge. The most abundant fish-eating birds at this site are Great Blue Herons (*Ardea herodias* Linnaeus) and Belted Kingfishers (*Ceryle alcyon* Linnaeus). Thirty-three fish species were recorded at the two streams. The most common species, in decreasing order of abundance, were blunt-nose minnows (*Pimephales notatus* Rafinesque), striped shiners (*Luxilus chrysocephalus* Rafinesque), central stonerollers (*Camptostoma anomalum* Rafinesque), hornyhead chubs (*Nocomis biguttatus* Kirtland), and sand shiners (*Notropis stramineus* Cope).

Our experiment manipulated one factor, predation intensity, with three levels of that factor: reduced, ambient, and elevated. Each of these levels was replicated across four different sites (two sites per stream), chosen for their similarity in habitat characteristics, trophic structure, and accessibility to avian predators. The design structure was a randomized complete block design, with each site serving as a block. Within each stream, treatment areas were selected based on similarity of within-stream and riparian characteristics. Each treatment area was ~ 12 m wide \times 60 m long (720 m²), with depths ranging from 12 cm in riffles to 102 cm in pools. Reaches with reduced predation consisted of 3.81-cm plastic bird netting suspended ~ 1.2 m above the water surface and stretched across the stream. Additional netting on the upstream and downstream ends was suspended just above the water surface to exclude wading birds, while still allowing fish movement. Every two weeks, litter that accumulated on top of the netted sections was placed into the reaches to minimize differences in litter input among treatments. Ambient reaches were unmanipulated sections of stream. Reaches with elevated predation had two types of perches added to encourage kingfisher predation: wire stretched across the stream and a wooden dowel rod attached perpendicularly to a fence post. Four wires and four fence posts were evenly spaced throughout the study reach to maximize kingfisher access. Treatments within each reach were separated by at least 120 m. Blocks on Jackson Creek and Prairie Creek were separated by 2.5 km and 11.5 km, respectively, with a number of shallow riffles between each block, making movement between blocks unlikely. Each block was located in the breeding territory of different kingfisher breeding pairs, which we determined by repeatedly walking along the stream and noting when kingfishers turned around (Davis 1982). We also suspect that each block was visited by a unique group of Great Blue Herons. A rookery is located on the Midewin property, and contained 14 nests in 2001 (J. Steinmetz, *personal observation*), thus over two dozen herons were nesting nearby. Although

herons can move up to 15 km to reach foraging grounds (Gibbs 1991), adult herons usually establish specific feeding territories (Butler 1992), which typically range in size from 0.129 km (Bayer 1978) to 1.37 km (Peifer 1979) of shoreline. Since our blocks were separated by at least 2.5 km, it seems likely that different herons used each block.

Behavioral observations of avian predators were conducted throughout the experiment, using a combination of live observers and videotaping. These observations ensured that the treatments were having their intended effect, and provided information on time spent foraging, number of prey taken, and predation pressure on prey populations (Steinmetz et al., *in press*). Birds captured significantly fewer fish in the reduced treatment (0.2 ± 0.2 [mean \pm 1 SE] fish/day) than in the ambient areas (2.44 ± 0.503 fish/day), which had significantly fewer captures than the elevated treatments (4.65 ± 0.689 fish/day). A complete description of the behavioral observations and bird predation rates is provided elsewhere (Steinmetz et al., *in press*).

Fish abundance in each treatment area was estimated using three pass removal estimates (Li and Li 1996). The entire study reach was enclosed with 5-mm block nets, and three passes were made using two Smith-Root (Smith-Root, Vancouver, Washington, USA) model 12 backpack electrofishers. Each fish captured was identified to species, its total length was measured, and it was released back into the study reach. The experiment ran for 60 days, from mid-July to mid-September, with fish abundance measured at the start and end of the experiment.

We analyzed effects of the treatments on total numbers of fish, mean size of fish, and numbers of certain size classes. We conducted species-specific analyses on the five most abundant taxa, which together comprised 77% of the total fish captured. The remaining 28 recorded species made up $<5\%$ each of the total fish captured and did not occur in all reaches. We thus excluded them from the analysis. We divided the most abundant species into size classes based on total length. Previous diet studies indicated that piscivorous birds usually fed on certain size classes of the most abundant prey (Butler 1992, Hamas 1994). We chose a 40-mm size interval because the preferred prey size of kingfishers is 80–120 mm total length (Hamas 1994), which is well within the range of prey sizes consumed by herons (Butler 1992). The 0–40 mm size class was excluded from all analyses because very few fish from any species were found in this size class in late summer–early fall. For each analysis, we subtracted the value for each treatment area at the start of the experiment from the value at the end, and used MANOVA or ANOVA on these differences. Normal probability plots and Levine's tests indicated that transformation

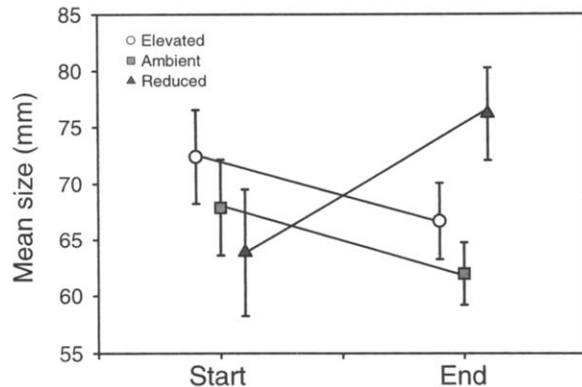


FIG. 1. Mean body size (total length ± 1 SE, $N = 4$) at the start and end of the experiment for the five most abundant species combined (bluntnose minnows, striped shiners, central stonerollers, hornyhead chubs, and sand shiners).

of the data was unnecessary. In all analyses there were no significant block effects (either for stream or site within stream), so the blocking term was dropped from the model. All analyses were conducted with SYSTAT 7.0 (SPSS, Chicago, Illinois, USA).

RESULTS

The most dramatic way top predators affect prey is by reducing the total numbers in an entire trophic level. To test for this we used a MANOVA, with total number of all species, plus total numbers for each of the five most abundant species as the response variables. We found no significant treatment effects (Pillai Trace; $F_{10,12} = 0.697$, $P = 0.727$).

Predators commonly affect only a subset of their potential prey items (Polis et al. 2000), and we did find predator effects for two common species, striped shiners and central stonerollers. Of the 33 species we recorded in the two streams, striped shiners and central stonerollers comprised 13% and 12%, respectively, of the total fish captured, and they were the second and third most abundant species. The most abundant species was the bluntnose minnow (37%). However, the largest bluntnose minnow was 94 mm and only 4% were larger than 80 mm. In contrast, 25% of striped shiners and 31% of stonerollers were larger than 80 mm.

If predators preferentially consume either the smallest or largest size classes, they may alter the average size of a prey population (Sogard 1997). We tested for this using a two-way ANOVA on the difference in mean body size (total length) between the start and end of the experiment for each of the five most abundant species and found a significant bird predation effect (Fig. 1). By the end of the experiment, the mean size in the elevated and ambient areas decreased, while the size

in the reduced areas increased ($F_{2,45} = 6.393$, $P = 0.004$; Fig. 1). There was no significant species \times treatment interaction ($F_{8,45} = 1.823$, $P = 0.098$); however, the changes appeared to be driven largely by striped shiners and central stonerollers (Fig. 2).

Examining average sizes can mask potential effects on individual size classes. We thus used a MANOVA to test for effects of bird predation on the number of individuals in different size classes. We limited this analysis to striped shiners, central stonerollers, and hornyhead chubs, as both bluntnose minnows and sand shiners were predominantly (>90%) in a single size class (40–80 mm). The MANOVA was significant (Pillai Trace; $F_{4,18} = 7.213$, $P = 0.034$), so we examined the protected univariate ANOVAs to identify which specific effects were significant. There were significant bird predation effects for the 80–120 mm size class for both striped shiners ($F_{2,9} = 4.297$, $P = 0.049$; Fig. 3) and central stonerollers ($F_{2,9} = 5.234$, $P = 0.031$; Fig. 3). The bird predation effect on the 120–160 mm size class of stonerollers was marginally significant ($F_{2,9} = 3.167$, $P = 0.091$).

DISCUSSION

We show that avian predators significantly altered the size distribution of the five most abundant prey items (Fig. 1), as well as decreasing the numbers of 80–120 mm striped shiners and central stonerollers (Fig. 3). Diet studies also show that avian predators usually consume certain size classes of the most abundant fish species (e.g., 80–120 mm total length for Belted Kingfishers [Salter and Lagler 1946], 100–200 mm total length for Great Cormorants [Hatch et al. 2000]). Because of their smaller size, the most numerically abundant species in our study, bluntnose minnows, probably escaped predation because birds were

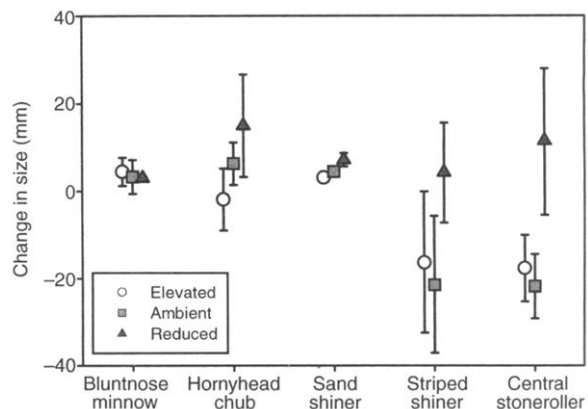


FIG. 2. Mean change in body size (ending total length minus starting total length) for each of the five most abundant species. Data are means ± 1 SE ($N = 4$).

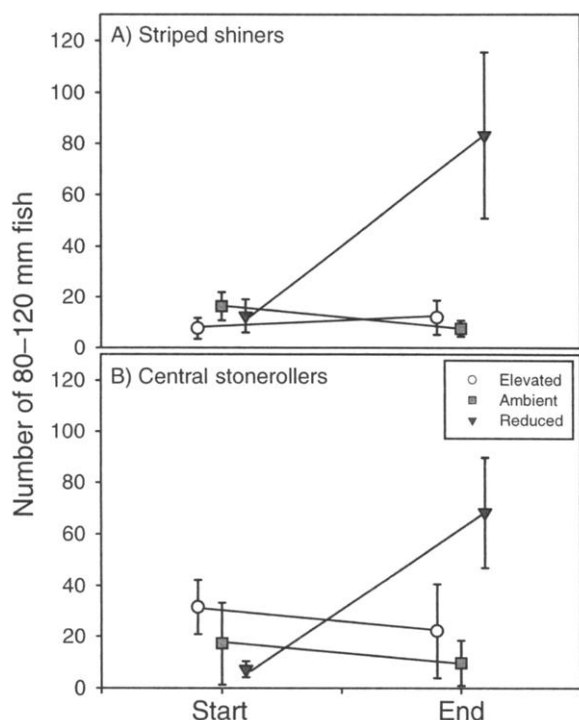


FIG. 3. (A) Total number of 81–120 mm striped shiners in each treatment at the start and end of the experiment. (B) Total number of 81–120 mm central stonerollers in each treatment at the start and end of the experiment. Data are means ± 1 SE ($N = 4$).

consuming larger and more energetically rewarding fish.

The difference between the netted reaches and the other treatments can be explained in three ways: (1) birds consumed prey in the control and perch treatments, thus leading to decreased abundance of 81–120 mm size classes in these sections; (2) fish emigration was lowest from the netted reaches, resulting in higher numbers of fish there; or (3) a combination of consumption and emigration may have caused the differences among the treatments.

We believe a combination of direct mortality and prey emigration was responsible for our results. First, behavioral observations indicated that birds were consuming fish (Steinmetz et al., *in press*). In fact, kingfishers and herons could have consumed more striped shiners and central stonerollers than we estimated were present in the elevated treatment areas (Table 1). Thus some fish immigration into the reaches likely occurred; however, it should not have differed among treatment areas. Fish use several cues to evaluate habitat suitability (substrate, depth, and flow; Kramer et al. 1997) that can only be assessed after arriving at a reach. It is thus likely that some of the differences in final prey

densities among treatments were due to decreased emigration from, not immigration to, the reduced predation treatment. Recruitment differences among treatments were unlikely since fish numbers were similar in all reaches in July, and all of these species had finished reproducing at that point. Future studies will be needed to determine the relative importance of direct predation and predator avoidance in driving the observed size-specific responses to predation.

Terrestrial predators are typically overlooked as a factor that can mediate the effect of insectivorous fish on their prey. For example, in the debate about whether fish regulate invertebrate prey populations in streams (Wooster 1994, Dahl 1998), not a single author has considered the role of avian predators. If birds and other terrestrial predators (e.g., raccoons, mink, otters) play widespread, functionally significant roles in aquatic food webs, then to fully understand aquatic food web dynamics, aquatic ecologists need to increase the scale of their studies to include wide-ranging avian predators and the landscape characteristics that influence their foraging behavior. For example, avian predator impacts may vary with proximity to nesting sites, which in turn is influenced by physical and biotic factors in the terrestrial landscape.

In conclusion, we showed that avian predators can significantly impact prey species in streams. It is therefore crucial that these overlooked predators be considered more fully when attempting to understand the structure of stream assemblages and aquatic food webs. The next step is to determine if the seasonal impacts we observed affect long-term prey population dynamics, and if impacts on fish affect other portions of the food web.

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TABLE 1. Estimated prey consumption by kingfishers and herons during the experiment and prey density in each treatment.

Treatment	Estimated prey consumed (no./720 m ²)	Total striped shiner and central stoneroller density (no./720 m ² ± 1 SE)	
		July	September
Reduced	12	61 \pm 18	321 \pm 71
Ambient	131	86 \pm 50	201 \pm 75
Elevated	242	78 \pm 24	146 \pm 66

Notes: Numbers represent means of four replicates per treatment. Prey consumption estimates are based on an average of 20 hr of behavioral observations per section and are for all fish species combined. Prey densities are based on three pass removal estimates. For further details see *Methods*.

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