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Facilitation between herons and smallmouth bass foraging on common prey

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Abstract Understanding how multiple predators affect one another and their shared prey is an increasingly important goal for ecologists examining predator–prey dynamics and food-web structure. In a field experiment, we examined the outcome of interactions between terrestrial and freshwater predators foraging for the same prey in two temperate North American streams. We used a factorial design to examine the combined foraging effects of herons and smallmouth bass on striped shiners and central stonerollers. We found that there was facilitation between the two predators, resulting in risk-enhancement for the prey species, with particularly pronounced effects on the smallest (<70 mm) size classes. Facilitation is the least well-documented predator–predator interaction and has not been quantitatively demonstrated for freshwater and terrestrial predators. Our results indicate that bass may gain a net benefit from the presence of wading birds such as herons and egrets, and that concerns about the negative effects of birds on fish stocks through competition may be unwarranted.

Keywords Multiple predators · Risk-enhancement · Non-additive · *Ardea herodias* · *Micropterus dolomieu*

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Introduction

Ecologists have traditionally focused on interactions between species pairs to gain insight into predator–prey dynamics and food-web structure. However, over the last two decades, there has been increasing interest in how larger networks of species interactions produce emergent properties (e.g. Soluk and Collins 1988; Werner 1992; Wootton 1994; Morin 1995; Vance-Chalcraft and Soluk 2005a, b; Griffen and Byers 2006). Perhaps the area where this has received the most attention is in the growing number of studies involving multiple predators (reviewed in Sih et al. 1998; Relyea 2003).

When more than one predator species forages on a common prey, there can be three types of interactions between the predators: neutral interactions, interference, or facilitation. Neutral interactions occur when the predators do not affect each other's foraging rate; this results in additive effects of the predators on their prey (e.g. Weissberger 1999; Sokol-Hessner and Schmitz 2002; Vance-Chalcraft 2003). Interference or facilitation typically leads to non-additive effects of the predators on prey. Interference occurs when at least one predator reduces the other's foraging rate; this leads to risk reduction and increased survival or fitness for the prey (e.g. Soluk and Collins 1988; Wissinger and McGrady 1993; Crowder et al. 1997; Stelzer and Lamberti 1999; Siddon and Whitman 2004; Vance-Chalcraft et al. 2004; Vance-Chalcraft and Soluk 2005a, b). Interference can occur in a number of different forms, including exploitative competition (Kohler 1992), interference competition (Wissinger and McGrady 1993) and asymmetric competition (Englund et al. 1992). Facilitation occurs when at least one predator enhances the other's foraging rate; this leads to risk enhancement and decreased survival or fitness for the prey (e.g. Soluk 1993; Losey and Denno 1998; Eklöv and VanKooten 2001; Bruno et al. 2003).

There is evidence that each of these outcomes occurs in a wide variety of taxa (reviewed in Sih et al. 1998; Werner and Peacor 2003), therefore the current emphasis is on the prevalence of these three types of interactions, and under what conditions each occurs. It is particularly important to understand under what conditions additive versus non-additive outcomes occur. If additive effects are more common than non-additive ones, understanding and predicting food-web dynamics becomes much easier. But given that non-additive effects do occur, it is important to know under what conditions they arise so that we can improve predictions about community structure (Sih et al. 1998). For example, Dickie et al. (2005) argue that when competition and facilitation vary spatially, the resulting mosaic of positive and negative interactions may increase species diversity. Understanding how multiple predators interact also has important management implications for areas such as biological control and conservation

management (Losey and Denno 1998; Müller and Brodeur 2002).

Multiple predator effects are certainly important in aquatic communities. Many different predator types feed in aquatic systems. In North America these include birds such as kingfishers (Family Alcedinidae), herons (Family Ardeidae) and mergansers (Family Anseriformes); mammals such as raccoons (Genus *Procyon* Stor), mink (Genus *Mustela* Linnaeus) and otters (Family Mustelidae); reptiles such as snakes (Order Squamata) and turtles (Order Testudines); piscivorous fish such as bass (Family Centrarchidae) and trout (Family Salmonidae); and predatory invertebrates such as crayfish (Order Decapoda), dragonflies (Order Odonata), dobsonflies (Order Megaloptera) and stoneflies (Order Plecoptera) (Cushing and Allan 2001). Many of these predators share common prey, usually fish or crayfish, and therefore have the potential to directly or indirectly interact.

For stream-dwelling fish, a number of factors, individually or in combination, may contribute to their vulnerability to these predators, including availability of refuge habitats (cover or depth), morphological and behavioral defenses, and the presence of other predators. Cage studies have provided convincing evidence that large fish in shallower water are at great risk from terrestrial predators, and that there is strong selective pressure to use deeper habitats (Power et al. 1989, Harvey and Stewart 1991). In these studies, fish were enclosed in experimental cages at various depths, and the disappearance of larger fish from the shallower cages was attributed to terrestrial predators such as birds.

To avoid terrestrial predators such as birds, fish can take refuge in either deeper habitats or habitats with more cover. The effect of birds will then be dependent upon the patterns of refuge use and the relative proportions of these habitats within the home range of the prey species. The impact of terrestrial predators will increase as the proportion of risky/safe habitat increases. Several costs may be incurred when fish shift to habitats where they are less vulnerable to terrestrial predators. One cost is that a "safer" habitat from birds may support large piscivorous fish, and so certain size classes of prey may have to choose

between predation risks. For example, juveniles of several species of fish restrict their distribution to shallow habitats in the presence of adult smallmouth bass, *Micropterus dolomieu* (Linnaeus) (Schlosser 1987).

One widely recognized pattern in stream ecology is attributed to these conflicting pressures from terrestrial and aquatic predators: larger fish are generally found in deeper water, and smaller fish in shallower water (Power 1987; Schlosser 1987; Harvey and Stewart 1991). The explanation for this is that small fish are not energetically rewarding to avian and mammalian predators, but are highly vulnerable to aquatic piscivores such as bass. As fish grow, they become increasingly vulnerable to terrestrial predators, and decreasingly vulnerable to gape-limited aquatic predators. Thus the risk of predation from birds and piscivorous fish induces an ontogenetic habitat shift in their prey.

Despite wide recognition of this pattern and acceptance of the hypothesized mechanism, few studies have experimentally looked at the combined effects of terrestrial and aquatic predators on shared prey in a freshwater system. Crowder et al. (1997) examined the effects of terrestrial and aquatic predators on prey in an estuary system. Wading birds and flounder interfered with one another, producing a non-additive effect on their common prey in the form of risk-reduction.

Exactly how avian predators and piscivorous game fish interact is an important issue for fishery managers concerned with increasing numbers of fish-feeding birds, such as herons (e.g. Glahn et al. 1999, 2000), which may directly consume game fish or compete with them for common prey. This research experimentally examines whether wading birds and smallmouth bass interfere with, are neutral towards, or facilitate one another.

Methods

The study took place in August and September, 2001, at Prairie Creek at Midewin National Tallgrass Prairie, northeastern Illinois, USA. Prairie Creek is a third order stream fed primarily by surface runoff, shallow groundwater, and field tile discharge. Substrate is primarily gravel and coble, with sections of sand and silt. The main wading birds in this system are the great blue heron, *Ardea herodias* (Linnaeus), green heron, *Butorides virescens* (Linnaeus), and great egret, *Ardea alba* (Linnaeus), and the main piscivorous fish is smallmouth bass, *Micropterus dolomieu* (Linnaeus).

The experiment was similar in design to those conducted by Power et al. (1989) and Harvey and Stewart (1991) except that we manipulated both avian and fish predators. The experiment was a standard 2×2 factorial design for investigating additive versus non-additive effects of predators on prey (e.g. Sih et al. 1998). The two treatments were avian predator presence/absence and piscivorous fish (smallmouth bass) presence/absence, resulting in four possible treatment combinations (no predators, bass alone, herons alone, or both predators present).

Cages were 3×2 m, constructed out of PVC pipe, heavy plastic screening, and anchored in place with 0.64 cm rebar. All four sides and the bottom were covered with 0.63 cm^2 black plastic screening. This mesh size allowed for invertebrate movement into and out of the cages while restricting prey movement. Depending on the treatment, whole or partial regions of the cages were covered with 3.8 cm plastic netting to prevent bird access. Twenty-four medium-sized rocks were evenly spaced throughout each cage to provide cover for the prey.

Cages were placed in the stream along a depth gradient, so that one end of the cage was in water <10 cm, sloping down to a depth of 54 cm or greater. This created a depth gradient in the cages such that in shallow areas prey was vulnerable to birds (Power et al. 1989; Hamas 1994), while in deep areas they were vulnerable to bass (Schlosser 1987). Mesh netting (5.1 cm) placed on top of the cages prevented bird access in the appropriate treatments. Additionally, a coarse mesh divider (5.1 cm mesh) divided the cage in two (parallel to the short axis), so that prey were free to move back and forth, but bass were restricted to the deep, and wading birds to the shallow portions of the cage (after Schlosser 1987). Since wading birds are ineffective predators in water greater than 30–

50 cm (Kushlan 1978; Butler 1992; Davis and Kushlan 1994; Glahn et al. 2000) and adult small-mouth bass are typically found in deeper pools (Schlosser 1987), this separation prevented any unusual interaction between herons and bass. Additionally, bass of the size used in this experiment (mean total length = 325.8 ± 9.3 mm, one bass per cage, with different bass being used for each treatment) are rarely preyed upon by herons. Diet studies indicate that herons mostly consume prey between 100–200 mm (e.g. Glahn et al. 2000). Wading birds are unlikely to cause major behavioral changes in these larger bass. Bass over 300 mm in length show only minor increases in cardiac output when exposed to heron models, indicating little physiological stress and fear of herons (Cooke et al. 2003). In contrast, cardiac output is much higher when similarly sized bass are exposed to osprey models, a predator to which even large bass are vulnerable (Cooke et al. 2003).

A total of four cages were used, with each of the four treatment combinations run in each of eight temporal blocks. Two cages were placed in each of two different sections of stream, separated by about 11.5 km. This ensured that bird treatments occurred in at least two different foraging territories. Thus for each replicate, we constrained the assignment of treatments to ensure that the two bird treatments were in different sections of stream. (Due to the relative sizes of the cages and stream, we could not place four cages in each of the two locations.) With this constraint, treatments were otherwise randomly assigned to cages in each temporal block.

Cages were stocked with natural densities of the two common prey from the stream: 20 striped shiners, *Luxilus chrysocephalus* (Rafinesque) and 10 central stonerollers, *Campostoma anomalum* (Rafinesque). Prey were measured to the nearest mm before being placed in the cage. Three different size classes were used: Small (mean: 72.7 ± 0.31 mm), Medium (mean: 97.0 ± 0.36 mm), and Large (mean: 128.2 ± 0.80 mm). The sizes and densities stocked in the cages reflected natural densities and size ranges occurring in the stream during the time of the study. Densities for each size class were: Small, 8 shiners and 4 stonerollers; Medium, 8 shiners and 4 stonerollers; and Large, 4 shiners and 2 stonerollers. Large prey were stocked at half the density of small prey due to

naturally lower abundances. Ratios of bass to striped shiners/stonerollers were similar to those observed in the field. In the field, the ratio of total striped shiners and central stoneroller to bass 150 mm or greater in size was approximately 36:1, while in our experimental cages it was 30:1. Bass were collected from Prairie Creek near the study sites and added to the cages immediately after capture to mark the start of the experiment. This ensured that both herons and bass were in natural states of hunger at the start of each experiment.

We conducted behavioral observations on 6 days throughout the study period to determine if birds were actually foraging in the cages. Vehicles were used as blinds and observations were made through 8×32 mm binoculars. The type of bird, number of strikes, and number of kills in each cage were recorded.

Trials were run for 2 days. Duration was determined by the results of preliminary studies, which indicated that 25–50% of prey were depleted from the cages with both bird and bass predators in this time period. After 2 days remaining prey were counted and their total lengths were recorded. Lengths were translated into mass using length–mass regressions developed for these species in this stream. To determine these regressions, the previous year 43 striped shiners and 23 central stonerollers were collected, frozen, and brought back to the lab to be measured and weighed. Length–mass relationships were determined using a quadratic regression calculated with SigmaPlot 4.0. Lengths used for calculations were total lengths (mm) and weights were wet weights (g) (Striped shiners: $R^2 = 0.98$; $P = < 0.001$. Equation: Wgt = 7.98–0.0295 (Lgth) + 0.0032 (Lgth)^2; Central stonerollers: $R^2 = 0.97$; $P = < 0.001$. Equation: Wgt = 5.92–0.24 (Lgth) + 0.0029 (Lgth)^2).

Response variables included number and proportion of fish missing, average size of missing fish, and biomass of missing fish. To protect against running two ANOVAs, we first ran a MANOVA with proportion of prey missing (after Krupa and Sih 1998) and biomass of missing prey as our response variables. If the MANOVA was significant, we then ran individual univariate ANOVAs on proportion of prey missing and biomass of prey missing. We also conducted a

separate MANOVA on the proportion of prey surviving in each of the three size classes, to look for size-specific effects. We included two blocking variables in the models: replicate (temporal block) and location (for the two locations in the stream). The analysis was done on log-transformed data, using Systat 10.2 (SYSTAT Software Inc. 2002). Levine's tests and normal probability plots indicated that the transformed data met the assumptions of normality and equal variance. Using log-transformed data also tests for multiple predator effects using a multiplicative risk model (Soluk and Collins 1988). It is preferable to test for multiple predator effects with this model as opposed to a purely additive model because it accounts for the fact that once a prey is eaten, it is unavailable to the second predator (Soluk and Collins 1988; Sih et al. 1998).

If birds and bass are neutral in their interactions we would expect a non-significant bird × bass interaction in the ANOVAs. If they interfere with one another we would expect a significant bird × bass interaction, with fewer prey consumed than predicted from an additive model. Lastly, if they facilitate one another we would expect a significant bird × bass interaction, with more prey consumed than predicted from an additive model.

Results

The behavioral observations indicated that herons were the only birds consuming prey in the cages. We watched cages on six different mornings, from approximately 07:30 to 14:30, 3 days at each of the two locations, with an average of 6.89 (±1.04 SE) hours of observations on each day. We saw herons feed in the cages on 5 of the 6 days. Four visits were by great blue herons, and one was by a green heron. There was an average of 2.4 (±0.4 SE) strikes and 1.6 (±0.4 SE) kills per bird per visit, with each visit lasting between 10 and 20 min. Based on these observations, in a 12-h day, herons should consume about three fish, or a total of six fish during the 2-day trials. These results agree with our numerical data on number of prey missing from the cages. In the bird-only cages, we found that approximately 18% of 30

fish, or 5.4 prey per 2 days, were consumed by herons.

The initial MANOVA was significant for bird, bass, and bird × bass effects (Wilks' Lambda, Pillai Trace, and Hotelling–Lawley Trace, with df = 2,19; $P < 0.001$ for all three tests). We found significant treatment effects on both the proportion of prey missing and biomass of missing prey (Tables 1, 2; Figs. 1, 2). There were no significant block effects for replicate or location. For the analysis of proportion of prey missing, there were significant effects for birds, bass, and the bird × bass interaction (Table 1, Fig. 1). Post-hoc tests showed that the bird-only and bass-only treatments did not differ (Fisher's LSD, $P = 0.754$), while all other treatment combinations were significantly different from one another (Fisher's LSD, $P < 0.001$). In both the bird-only and bass-only treatments, approximately 15% of prey were consumed, while in the bird + bass treatments about 40% of prey were consumed. The multiplicative risk model predicts that, if these predators had additive effects on prey, only 29% of prey should have been consumed in the bird + bass treatment.

The analysis of size classes indicated that there were significant effects of the bird-only treatments and bass-only treatments on all three size classes, but only significant bird + bass effects for the 70 mm size class (Table 3, Fig. 3). Thus, while there was a non-additive, risk enhancement effect for the 70 mm size class, there were only additive effects for the other two size classes.

We saw different results when we analyzed the biomass consumed by the two predators (Fig. 2). Post-hoc tests showed that except for the bird-only and bass-only treatments (Fisher's LSD, $P = 0.114$), all other treatment combinations were significantly different from one another (Fisher's LSD, $P \leq 0.001$). Although the numbers of prey consumed by birds and bass was similar (Fig. 1), birds tended to consume a higher biomass of prey than bass (Table 2, Fig. 2). Unlike the proportion of prey missing analysis, when looking at proportion of biomass consumed there was not a significant bird × bass interaction. Thus although a higher biomass of prey was consumed than expected based on the multiplicative risk model (Fig. 2), there was no statistical evidence for facilitation (Table 2).

Table 1 Results of univariate two-way ANOVA on log transformed proportion of prey missing from cages where prey were exposed to wading birds, adult bass or both bird and bass predators

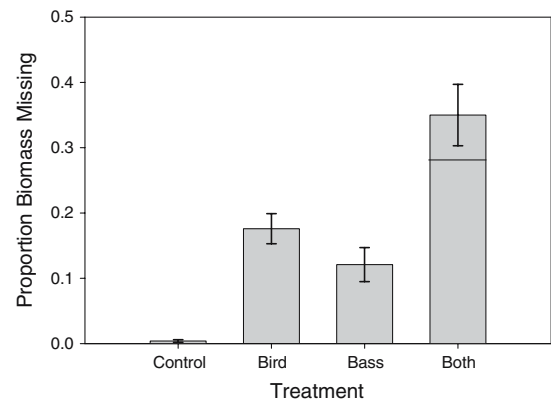| Source	SS	df	MS	F	P
Replicate	0.004	7	0.001	1.517	0.218
Location	<0.001	1	<0.001	1.268	0.274
Bird	0.040	1	0.040	112.41	<0.001
Bass	0.037	1	0.037	103.10	<0.001
Bird × Bass	0.002	1	0.002	6.010	0.024
Error	0.007	20	<0.001		

Table 2 Results of univariate two-way ANOVA on log transformed proportion of prey biomass missing from cages where prey were exposed to wading birds, adult bass or both bird and bass predators

Source	SS	df	MS	F	P
Replicate	0.038	7	0.005	1.57	0.201
Location	0.011	1	0.011	3.19	0.089
Bird	0.232	1	0.232	67.42	<0.001
Bass	0.119	1	0.119	34.54	<0.001
Bird × Bass	0.001	1	0.001	0.402	0.533
Error	0.069	20	0.003		
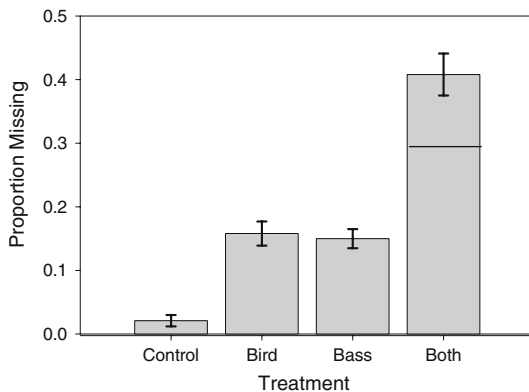
Fig. 1 Proportion of prey missing. The horizontal line on the "Both" treatment indicates expected proportion missing in the combined predator treatment if the effects of the predators are additive. Expected calculation based on the multiplicative risk model. Error bars are ±1SE

Fig. 2 Proportion of biomass missing. Biomass estimates based on measured total lengths converted to weights using the length–mass regressions given in the text. The horizontal line on the "Both" treatment indicates expected proportion missing in the combined predator treatment if the effects of the predators are additive. Expected calculation based on the multiplicative risk model. Error bars are ±1SE

Discussion

This is the first study to document numerical facilitation between aquatic and terrestrial predators in a freshwater system. Although it is unclear whether both predators benefited equally, we suspect that bass benefited more. An additional 7.75 prey were consumed in the combined predator treatments compared to the bass-only treatment (4.5 prey per cage versus 12.25 prey per cage, a 172% increase, Fig. 1). Furthermore, the

facilitation was driven largely by the 70 mm size class—the size class most vulnerable to bass (Fig. 3). It is likely that during the relatively short periods when birds were present, they forced the prey into deeper water facilitating the increased consumption by bass. If the reverse were true, and bass were facilitating consumption by birds, we would have expected the birds to obtain more

Table 3 Results of multivariate and univariate ANOVA of predator effects on the log transformed proportion of prey missing from three prey size classes

Predator Treatment	Response Variable	Source	SS	df	F	P
Birds-only	MANOVA	Model	0.148[a]	3,19	36.54	<0.001
	70 mm	Model	0.045	1	48.12	<0.001
		Error	0.019	21		
	100 mm	Model	0.036	1	36.41	<0.001
		Error	0.019	21		
	130 mm	Model	0.038	1	19.02	<0.001
		Error	0.039	21		
Bass-only	MANOVA	Model	0.138[a]	3,19	39.65	<0.001
	70 mm	Model	0.070	1	74.73	<0.001
		Error	0.019	21		
	100 mm	Model	0.025	1	25.19	<0.001
		Error	0.019	21		
	130 mm	Model	0.018	1	9.211	0.006
		Error	0.039	21		
Bird + Bass	MANOVA	Model	0.708[a]	3,19	2.609	0.081
	70 mm	Model	0.006	1	5.956	0.024
		Error	0.019	21		
	100 mm	Model	0.001	1	0.716	0.407
		Error	0.019	21		
	130 mm	Model	0.001	1	0.620	0.440
		Error	0.039	21		

For each predator treatment, the MANOVA results (with each prey size class as the dependent variables) are presented first, followed by results of univariate ANOVAs for each size class

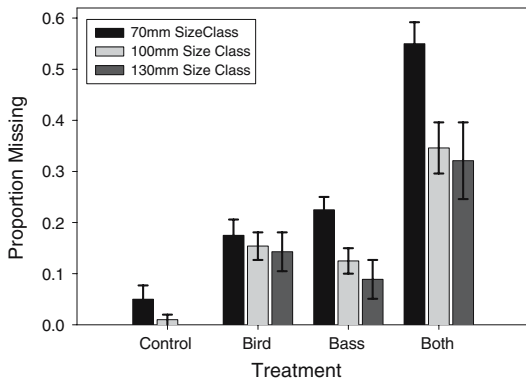[a] Wilks lambda, Pillai Trace and Hotelling–Lawley Trace showed similar results

Fig. 3 Proportion of prey consumed in each of the three size classes used. Error bars are ±1SE

than the 1–2 prey per cage visit that we observed. This result suggests that rather than negatively affecting bass populations, wading birds may increase prey capture by bass, thus alleviating some of the concerns that piscivorous birds negatively affect game fish (e.g. Feltham 1995; Kirby et al. 1996).

Because the smallest size class drove the numerical facilitation, we did not see evidence for facilitation when examining biomass. The trend for biomass (Fig. 2) was the same as for the numerical response (Fig. 1), with more prey consumed in the combined predator treatments than expected by an additive model, but it was not statistically significant. Because an equal number of small and large prey do not contribute an equal percentage of total biomass, the facilitative effects of the two predators on smaller prey were most likely swamped by the additive effects of medium and large prey (Table 3). These results stress the importance at looking not only at total prey consumed, but also size structure and biomass to understand the results of multiple predator studies.

Interestingly, we found that when birds and bass were alone, they consumed similar amounts of prey (Fig. 1). This suggests that when encountering a single predator, prey are equally vulnerable to both predator types, and that birds may be playing a more important role in regulating prey than is generally considered (Steinmetz et al. 2003).

Although it was not statistically significant, there was a trend for birds to consume larger fish

than bass (Fisher's LSD, P = 0.114). Because they consumed more prey in the medium and large size classes (Fig. 3), the average size of fish consumed by herons was 10 mm larger than fish consumed by bass, resulting in an average biomass consumed by birds of 57 g compared to only 38 g in the bass treatments (Fig. 2). In contrast, the smallest size classes were most vulnerable to bass (Fig. 3). These findings support the larger-fish-in-deeper-water paradigm (Schlosser 1987), which states that larger fish are more vulnerable to terrestrial predators, while smaller fish are more vulnerable to piscivorous fish.

It is unknown whether seasonal variation in the occurrence and strength of facilitation occurs. Our experiment was conducted in late summer, after young birds had fledged but before fall migrations (Butler 1992), so both adult and juvenile herons were foraging in the area. During the winter, bird predation levels drop substantially due to migration of the wading birds (e.g. Butler 1992), although belted kingfishers will remain as long as there is open water (Hamas 1994). Concurrently, fish metabolism decreases with low winter temperatures (Fry 1971), leading to decreased activity levels and foraging rates for bass. Thus winter predation could be minimal for both predators. In fact, one study found avian predation rates at aquaculture facilities to be minimal in winter (Glahn et al. 1999). In the spring birds are breeding and young will be fledging (Butler 1992; Hamas 1994), thus the number of prey taken per adult should be greater than in late summer. However, the streams are generally higher and more turbid during this time, which should create more refuge habitat (in terms of both depth and turbidity), and thereby reduce the strength of facilitation. Future studies should examine how these predator–predator interactions vary seasonally and how this variation affects prey population dynamics.

The type of predator interactions in our study is similar to those in the growing number of studies reporting predator facilitation. Facilitation usually occurs when two predators forage in different parts of a common prey's habitat, and the prey's main behavioral response to the predators is to shift microhabitats (Soluk 1993; Soluk and Richardson 1997; Losey and Denno

1998). Such habitat shifts have been documented in voles responding to raptor and weasel predators (Korpimäski et al. 1996), and in gerbils responding to snake and owl predator cues (Kotler et al. 1993). Thus when confronted with two predators simultaneously, the prey's refuge space is restricted and risk enhancement occurs. In our study, terrestrial predators foraged in shallow water, while aquatic predators foraged in deeper water, eliminating depth as a refuge. Predator facilitation has been documented in a number of other systems and taxa: stoneflies and fish foraging on mayflies (Soluk and Collins 1988; Soluk 1993); foliar-dwelling and ground-dwelling insects feeding on aphids (Losey and Denno 1998), two salamander species foraging on tadpoles (Morin 1995), and pike and perch feeding on roach (Eklöv and VanKooten 2001).

Not all situations where the prey face different predators in different microhabitats lead to facilitation. For example, water striders reduce their predation risk in the presence of centrachid sunfish and fishing spiders by reducing mating activity (Krupa and Sih 1998). This behavioral modification reduced their vulnerability and decreased their encounter rate with both predators. In a study similar to ours, birds and a fish predator (flounder, *Paralichthys lethostigma* Jordan and Gilbert) caused their common prey (spot, *Leiostomus xanthurus* Lacepède) to aggregate more tightly when both predator types were present (Crowder et al. 1997). The result was predator interference, rather than facilitation, with fewer prey being consumed in the combined predator treatment than what would be predicted based on the additive model. These studies suggest that a behavioral modification of the prey can alter the expected outcome from risk enhancement to risk reduction.

One important difference between our study and that of Crowder et al. (1997) was that birds by themselves did not have a significant effect on prey abundance in their study. If prey are not particularly vulnerable to birds, they may be able to effectively use shallow water as a refuge and decrease the chance for risk enhancement. Although we did not take formal observations in our study, we did not notice the aggregating response in striped shiners or central stonerollers

that Crowder et al. observed in spot. However, it is possible that the size of our cages (6 m^2) may not have allowed for the same behavioral responses that occurred in their larger estuarine areas (79 m^2).

The question remains, why does facilitation occur in some situations but not others? The answer may come from examining the question from the prey's perspective. Each of the possible predator–predator interactions translates into very different outcomes for prey populations: reduced prey survival (facilitation), additivity (neutrality), or increased prey survival (competition). Lima and Bednekoff's (1999) Risk Allocation Hypothesis suggests that prey respond not only to the presence/absence of predators, but also to temporal variation in predation risk. This variation can occur on a variety of time scales, including daily, seasonally, or with the lunar cycle (Lima and Bednekoff 1999; Sih et al. 2000). In a multiple predator context, prey are not likely to be in continuous contact with both predators, so the question becomes what is the relative probability of encountering each predator in their respective habitat? If a prey is equally likely to encounter both predators at the same time, then there should be selection for a strategy other than simply switching habitats. For example, there may be an equal probability of mortality from sunfish and spider predators for water striders. This may have led to a strategy of reducing activity in the presence of both predators (Krupa and Sih 1998). In our study, however, because birds were only present for short periods of time throughout the day, but were efficient foragers when present, prey may choose to avoid this high, but short-term predation risk by simply switching habitats. Indeed, some studies suggest than when faced with multiple predators, prey simply respond to the riskier predator (reviewed in Relyea 2003). This may be especially true when the exposure to the riskier predator is for shorter durations than for the less risky predator. Future work should examine how the Risk Allocation Hypothesis may help explain the circumstances leading to predator facilitation, competition, or neutrality.

In summary, this was the first study to document facilitation between freshwater and terrestrial predators. The results support the traditional explanation of the larger-fish-in-deeper-water paradigm and should ease concerns that wading birds such as herons and game fish are competing with one another for common prey. Future studies should be done to determine the mechanism of facilitation and to test the ideas on what sorts of predator–predator interactions can lead to facilitation and interference among predators. Too often complex ecological communities are managed based on simplified assumptions. If the effects of both birds and bass had not been considered in this study, we may have missed the counterintuitive result that loss of avian predators may actually harm bass populations in these streams. Understanding such complex relationships is important for both avian and fish conservation.

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