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Avian predators transmit fear along the air-water interface influencing prey and their parental care

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Running title: Birds control fish parental behavior

Abstract

The non-consumptive consequences of predators on prey behavior, survival, and demography have recently garnered significant attention by ecologists. However, the impacts of top predators on free-ranging prey are challenging to evaluate as the most common fright responses for prey is to leave the area of risk. Additionally, the top-down impacts of avian predators on aquatic environments are surprisingly overlooked. Here we investigated the non-consumptive effects of avian predators on parental care in sunfish (*Lepomis gibbosus*, L., 1758) through the use of a realistic model of a predatory bird, the osprey (*Pandion haliaetus*, L., 1758). Our predator model exacted dramatic metabolic fright responses and inducible defenses in experimental fish resulting in significant behavioral changes with respect to their parental care. Key parental behaviors including in-nest rotations and egg and nest maintenance were noticeably altered by predator

treatments demonstrating as much as an order of magnitude difference in parental performance, suggesting that even transient predation risk might decrease reproductive fitness. Our data provide important new insights on how the landscape of fear operates along the air-water interface and suggests that avian predators may have greater controlling effects on fish populations than previously thought.

Keywords: landscape of fear, *Lepomis gibbosus*, osprey, *Pandion haliaetus*, parental care, predator, predation risk, pumpkinseed

Introduction

Predation, the direct killing of prey, is one of the most fundamental and important concepts in ecology. Predators can transmit the fear of being killed (the risk of predation) throughout the ecosystem, and these ‘fear effects’ can significantly alter the behavior, energetics, and life histories of prey species (Lima and Dill 1990). Predators can also elicit phenotypic changes in morphology as well as behavior through increased vigilance and physiological stress (Lima 1998; Peckarsky et al. 2008). While such changes can reduce risk of mortality in the short term, these changes can also have negative consequences, such as decreased foraging, chronic stress, lower body condition, decreased investment in somatic growth, and even changes in demography (Zanette et al. 2011). These effects may, in fact, be more important than direct mortalities alone in shaping food-web patterns as they can represent a broader portion of the total effect predators have on prey (Creel and Christianson 2008).

Experimental investigations into this ‘ecology of fear’ are crucial for better understanding exactly how predators influence food-webs as well as ascertaining the drivers of ecosystem collapse that result when predators are removed from ecosystems. The latter has become increasingly important as top predators are being persecuted worldwide, resulting in ecological imbalance and human-wildlife conflict (Côté et al. 2004; Estes et al. 2011). However, manipulating large predators under natural conditions is inherently difficult due to their wide-ranging and cryptic nature, as well as their overall rarity in terrestrial and aquatic ecosystems.

Researchers often simulate predation risk by exposing prey species to visual, chemical, or auditory cues from predators, and then measure any variety of behavioral or physiological changes in the prey (Dill and Fraser 1984; Sheriff and Thaler 2014). Studies simulating predation risk have documented significant changes in prey behavior, increased physiological stress associated with acute risk of mortality, and decreased reproductive activity among invertebrates (Matassa and Trussell 2014), fish (Werner et al. 2015), reptiles (Amo et al. 2004), birds (Ghalambor et al. 2013), and mammals (Curé et al. 2013). Collectively, these studies demonstrate that simulating predator presence can be an effective approach for measuring the effect of predators on wild prey, thereby providing researchers a valid tool for increasing our knowledge of risk effects across species.

While many terrestrial and avian predators kill and consume aquatic prey (e.g., Dalton et al. 2009), the non-consumptive effects of these interactions remain relatively understudied, particularly for large bird predators (Fauchald et al. 2000, Steinmetz et al. 2003, Zydelski and Kontautas 2008; but see recent work by Hill and Heck 2015, Pepino et al. 2015). Here we used a realistic model of an osprey (*Pandion haliaetus*, L., 1758), a predatory fish-specialist throughout most of its range, to test the hypothesis that the presence of aerial predators can significantly

alter fish parental behavior. As a focal prey species, we used nesting pumpkinseed sunfish (*Lepomis gibbosus*, L., 1758), a common prey for osprey throughout their range (Häkkinen 1978; Steeger et al. 1992; Francour and Thibalt 1996), due to their extensive parental care and thus high site/nest fidelity while nesting during the reproductive period. The reproductive period is an excellent time to test the effects of predation on fitness (offspring survival versus self-maintenance trade-off) as guarding males (a) do not forage or leave the nest site except under extreme duress and (b) display a range of quantifiable behavioral traits. We discuss our findings as they pertain to the literature on risk effects and their influence on fish fitness (Ryan et al. 2013), as well as the controlling impacts of top avian predators on aquatic food-webs.

Materials and Methods

Study sites

This study was conducted from 14 to 24 May 2014 in Lake Opinicon, located in eastern Ontario Canada (44°33'56.0" N, 76°19'23.6" W). Lake Opinicon is a relatively shallow and mesotrophic system with a large proportion of highly vegetated littoral zones (maximum depth ~11 m, surface area 890 ha). To understand predator-prey interactions between piscivorous bird predators and sunfish at this site, we focused our efforts on osprey (*Pandion haliaetus*) and pumpkinseed sunfish (*Lepomis gibbosus*). Osprey preferentially forage on sunfish in littoral zones of the lake, and the number of active osprey nests there have ranged from 5-10 per year since 2001 (QUBS staff, personal communication).

Experimental design

Field observations occurred along a shallow gravel/sand bar (~500 m long x 100 m wide) containing a high abundance of pumpkinseed nests with males guarding eggs in the littoral zone

of the central-western edge of the lake (an estimated 150 nests were constructed at the start of the study). All experiments were conducted between 1000 and 1400 hr under calm and sunny conditions. The depth of the sandbar ranged from 1-2 m, and the nesting substrate throughout this region was primarily comprised of sand-gravel. For the purposes of this study we focused on clean nests (i.e., excluding vegetation or rock-dominated nests) with males actively guarding eggs. Suitable nests were located via snorkeling by trained researchers (teams of 2), and marked with a white PVC identification tag (10 cm x 5 cm) on the outer rim. The total length (TL) of parental male sunfish was estimated *in-situ* by researchers since precise measurements of fish size were not possible without capture and thereby potentially unacceptable levels of disturbance. Parental males were within the size range (estimated TL = 120 – 200 mm) of fish prey for osprey (Häkkinen 1978; Francour and Thibault 1996); fish length classes were used (1-3; 1 = small, 120-140 mm; 2 = medium, 140-160 mm; 3 = large, > 160 mm) and the relative size of each overall egg mass was scored by the same snorkeling team (1-5, 1 = very few, 5 = very many). All nests we used contained an adult male and egg mass of unhatched, fertilized eggs that were yet to hatch (Colgan and Gross 1977). After each nest was selected and tagged, we then departed the nest area (i.e., 5-10 m away, outside the visual detection range of the fish) for a period of at least 90 seconds to mitigate disturbance to the fish before experimentation.

Each experimental series began with an aggression test that was conducted by one snorkeler, by placing a bluegill (100-140 mm total length; *Lepomis macrochirus*, Rafinesque, 1810, an active nest predator) housed inside a clear glass container (volume ~ 4 litres) on the edge of the nest for 60 seconds. The number of attacks (defined as any close rush, bump, or bite) made on the container by the parental male was recorded over the observation period, after which the jar was removed. This method is widely used to evaluate parental aggression in

centrarchid fishes (Zolderdo et al. 2016). One snorkeler then placed a small high-definition camera on the edge of the nest (GoPro Hero 3+, 48) and recorded fish behavior continuously for a period of 12 minutes. This 12 minute period consisted of three phases: (1) pre-stimulus, 5 minutes; (2) stimulus phase (presence/absence of predator model), 2 minutes; (3) post-stimulus, 5 minutes (Fig. 1). In phases (1) and (3), we chose a set of parental behaviors scored as metrics following Cooke et al. (2008) and Colgan and Gross (1977) as represented by (a) cumulative time outside the nest (seconds), (b) number of full (360°) in-nest rotations, (c) total number of spinal flares (defined as the erection of dorsal spines), (d) number of burst behaviors (defined as rapid, erratic swimming behaviors across the nest), and (e) total number of nest-maintenance behaviors (including any combination of tail fanning, mouthing of eggs, body-axis change to look at eggs). During phase (2), we quantified predation-risk-related behaviors (e.g., latency, defined as the average duration from when predator was introduced until fish demonstrated a marked behavioral response, in seconds), and recorded the total number of trips each fish made outside the nest, as well as the number of burst swimming behaviors and dorsal spine erections exhibited by each individual. Across all trials we also quantified the total number of individuals that temporarily left as well as the number of individuals that temporarily abandoned and returned versus never returned.

Predator simulation

Predator models used in phase two comprised an artificial osprey kite (112 cm wingspan, 45 cm head to tail, Jackite Inc, Virginia Beach, VA, USA) attached to a 6 meter telescopic pole by way of a 1 meter string (Fig. 2a). The model bird mimicked the colors, patterns, shape, and realistic flying manner (gliding and swooping behavior) of ospreys (following Swenson 1978). At the onset of phase two, a trained snorkeler slowly approached the nest from offshore until the

osprey kite was positioned above the center of the nest (Fig. 2b, about 6m away to minimize observer bias). For a period of two minutes we flew the osprey over the nest, using gentle movements to move the bird laterally and vertically (~2 meters above the nest; Fig. 2c). We chose this height because is a realistic simulation of how osprey hunt fish from above. After the final 5-minute post-predator phase (phase 3), we conducted a final aggression test using the same bluegill in the jar and again recorded the number of attacks over 60 seconds.

Controls and context

We also randomly performed a series of controls using the same experimental design as above but without using the osprey kite, therefore serving as the absence of the predator (phase 2). The observers maintained the same position in these controls as they did the other treatment, and snorkelers maintained a minimum distance of 3 meters away from the nest during all recording periods to minimize bias and disturbance. We did not find any active osprey nests within 2 km of the study area, and this region was actively monitored for external fishing activity and no fish exhibited signs of fishing-related injuries. Fishing for black bass (*Micropterus spp.*) is illegal during this period so anglers generally avoided littoral habitats.

Statistical analyses

To examine the acute behavioral responses of each fish during the predator exposure period (phase 2), we used t-tests to compare the total number of trips outside the nest, the number or burst swimming behaviors, and the number of dorsal spine erections between predator-exposed fish and control fish. We calculated the change in five behaviors (i.e., absolute between phase 1 and 3) for all fish across both treatments: rotations in the nest, nest attention/maintenance behaviors, total time spent outside the nest (seconds), dorsal spine

erections/flares, and attacks on bluegill (which were book-ended on phase 1 and 3). These data were then ranked to meet the assumptions of normality and homogeneity of variance (i.e., any statistical analyses were conducted on ranked data). The five behaviors were not mutually exclusive and thus, were compared between treatments (predator presence/absence) using a one-way multivariate analysis of variance (MANOVA). Subsequent ANCOVAs were run on each behavior/dependent variable to contrast mean behavioral ranks between treatments using estimated fish size and egg score as covariates. In phase 2 (the 2-minute stimulus period), we used student's t-tests to examine ranked differences in the total trips outside the nest, the number of burst swimming behaviours, and the number of dorsal flares between treatments (osprey presence versus absence). To promote context and relevance to behaviorally-meaningful information, all graphical plots present non-transformed data. All statistical analyses were conducted in SPSS at $p < 0.05$ level of significance.

Results

Thirty-eight trials (predator stimulus, $n = 21$; predator absence, $n = 17$) were conducted which resulted in a total of 456 minutes of video footage used for behavioral quantification and analysis. The mean fish latency to respond to the model was 7.9 ± 1.5 seconds. Predator-exposed fish had a higher number of trips outside the nest, burst behavior events, and dorsal spine erections during Phase 2, relative to control fish ($p < 0.001$, Fig. 3a-c). The before-and-after behavior of nesting male pumpkinseed was also significantly affected by the experimental predator treatments (MANOVA, $F_{1,34} = 17.70$, $p < 0.0001$, Fig. 4). Four of the five variables we subsequently investigated were the statistical drivers of this difference (Table 1). Changes among in-nest rotations and nest maintenance behaviors were significantly influenced by the predator treatment ($p < 0.0001$, Table 1). Pumpkinseed exhibited an average of 9.76 ± 1.37 fewer

rotations after being exposed to the predator cues, an order of magnitude fewer than when the cues were absent (Fig. 4a). Fish exposed to predator cues also showed an average of 5.05 ± 1.03 lower nest maintenance behaviors when compared to a slight positive change of 0.18 ± 0.47 nest maintenance behaviors when the fish were not exposed to predator cues (nearly 5 times fewer, Fig. 4b).

The erection of dorsal spines and total time spent outside the nest were also significantly affected by the treatment ($p < 0.001$, Table 1). The change in dorsal spine erections was 126% higher in predator-exposed fish relative to controls (Fig. 4c). Predator-exposed fish also spent an average of around 60 times more time (in seconds) outside the nest relative to controls (Fig. 4d). Changes in pumpkinseed attacks on the bluegill jar were not significantly affected by the treatment ($p = 0.232$). Neither fish body size nor egg score significantly affected any of changes in any of the five behaviors (Table 1).

Discussion

Our results experimentally demonstrate that the ‘fear’ of predators operates in three-dimensions and can be transmitted through the air-water interface. Moreover, we showed that avian risk effects can cause prey to alter key parental behaviors that occur during a critical life-history phase. Adult male pumpkinseed in this study responded to the simulated predation risk relatively quickly (i.e. < 10 seconds) and engaged in vigilance displays and avoidance behaviors that were prioritized over behaviors directly linked to fitness, including nest guarding and egg maintenance. This reveals that the threat of predation alone from avian predators can have direct effects on their prey, and indirectly on the prey’s offspring.

By coupling video recording with the introduction of predator risk effects, we were able to observe the onset and duration of a suite of behavioral “fight-or-flight” responses in parental pumpkinseed. During exposure to a stressor, in teleost fish, sensory input stimulates the hypothalamic-pituitary-interrenal (HPI) axis. Briefly, this includes an up-regulation and secretion of cortisol, the primary glucocorticoid, which mediates a host of physiological scale effects including energy mobilization, cardiovascular activity and protein synthesis; an essential process which works to mitigate the negative impacts of the stressor (reviewed in Barton 2002). Physiological effects of both cortisol and catecholamine secretion, under a predation threat, are likely to be mediating the behavioral responses observed here (Hawlana and Schmitz 2010). The visual presentation or detection of a predator represents an acute stressor for the prey species, with predator-induced fear effects having profound impacts on the physiology and survival of free-living animals (Pepino et al. 2015). Experimental fish in the present study exhibited significant increases in dorsal spine erection and burst swimming behaviors shortly after the predator was introduced (Fig. 3). Dorsal spines have evolved in fishes as a predator deterrence mechanism reducing prey susceptibility and foraging profitability by the predator (Huntington et al. 1994; Smith and Jan 1997). In pumpkinseed, high predation pressure can alter spine morphometrics representing an inducible defense mechanism (Januszkiewicz and Robinson 2007). Burst swimming behaviors are rapid, darting movements which occurred throughout the nest when the predator was overhead, and occurred nearly 4x more under the threat of predation (Fig. 3b) with a maximal individual value of 14 bouts. Both of these fright responses are presumably a flight response or used to deter and/or confuse predators, yet they undoubtedly carry associated metabolic costs when their excitation is prolonged (O'Connor et al. 2009; Connor et al. 2011). Fish also increased their trips outside the nest under the threat of predation

(Fig. 3c), presumably showing that the risk of mortality outside the nest is lower than when a predatory bird is circling overhead (indeed, the fish shape is strongly contrasted against the excavated nests). By exposing largemouth bass to a similar osprey model under controlled laboratory settings, Cooke et al. (2003) induced bouts of cardiac disturbance (i.e., bradycardia) in experimental fish, thus suggesting that the non-lethal costs of avian predation have profound implications for altering physiological state and elevating metabolism in centrarchids. Our results from the exposure portion of our experiment add behavioral perspectives to the findings from Cooke et al. (2003) that suggest avian predation risk is acute and profound for fish with direct consequences for present and future fitness.

Exposure to predators can also have sustained effects on prey in the absence of killing by changing the demography of their populations by altering birth rates and the survival of offspring (Preisser et al. 2005). Nesting and incubating prey species, offer a robust model for evaluating predation risk and associated trade-offs since the degree of parental care is directly related to the probability of offspring survival (Sargent 1988). Over the course of our experimental trials, we documented significant changes in nest-related behaviors that could affect egg health and survival. Most importantly, we detected an order of magnitude lower number of fish rotations and nearly 5 times lower nest-related maintenance behaviors under predation risk (Fig. 4a-b). In-nest rotations and nest maintenance (fanning of eggs, cleaning of nest) are the two most common behaviors exhibited by parental sunfishes (Miller 1963; Winemiller and Taylor 1982; Danylchuk and Fox 1996). In-nest rotations are a defensive, moving-sentry behavior to signal, ward-off, and maintain control of nests from nest predators (e.g., bluegill).

Across all trials, the fish in the phase 1 of the experiment ($n = 38$) swam an average rate of ~3 rotations per minute, which dropped by above 50% under predation risk (Fig 4d). Considering that nest defense in pumpkinseed has been directly linked to how well males sire their young (Rios-Cardenas and Webster 2005), this change may be significant to their overall reproductive fitness. The same could be said for the changes we observed in nest-maintenance behaviors (Fig. 4b) including significant decreases in nest-maintenance behavior such as fanning (Fig. 2c) which promote oxygen transfer to eggs as they develop, and time spent outside the nest (Fig. 4d) which leaves nests open to predation by surrounding egg predators. Dorsal flares significantly increased in fish after they were exposed to the predator model, a finding consistent with other work showing behavioral changes persist after exposure to predation risk in other vertebrates (Valeix et al. 2009). We realize this study only looked at real-time effects, and that we were not able to determine the chronic impacts that predation risk can have on fish fitness (however, this work suggests they may be appreciable).

Studies of predation risk on nesting birds have demonstrated that “intimidating” prey species through non-lethal predator cues can cause females to lay fewer eggs with a marked decrease in egg health and survival (Eggers et al. 2008; Travers et al. 2010; Zanette et al. 2011). While we did not directly assess egg health and/or survival over time, parental investment theory itself would support the notion that the decreased attention to eggs, higher rates of nest abandonment, and decreased attention to maintaining egg condition we documented do indeed result in some degree of lower egg survival and fitness. Therefore, we believe our results using a bird-fish model system provide an important real-time behavioral perspective to the important and growing body of experimental work on predation risk in vertebrates. This work also adds

behavioral insights to other recent work showing how birds can affect fish distribution (Ryan et al. 2013) and behaviour and survival (Hill and Heck 2015; Pepino et al. 2015).

By showing how, behaviorally, avian predators affect prey in a non-consumptive manner, we provide two new key insights into the ongoing discussion of the ecosystem-wide importance of predators: (1) the “landscape of fear” operates in three dimensions and transmits across mediums; and (2) the recovery of avian predators can restore an essential ecosystem service – predation risk. Ospreys are one of the greatest examples of conservation success in North America as their populations have recovered following decades of decline due to habitat loss and pollution from pesticide (Henny et al. 2010). Previously, little was known about the effects these raptorial birds have on prey and the greater-food web (Bierregaard et al. 2014). Here we show that their impacts on prey can be strong, therefore the recovery of their populations may have greater benefits on food-web stability than previously thought.

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Figure Legends

Figure 1. Conceptual diagram showing the experimental set-up used to assess the impacts of perceived avian predation risk on parental behavior in nesting male pumpkinseed (*Lepomis gibbosus*, L., 1758), broken down by the three phases of each experimental trial. White dishes represent nests. Controls did not receive a predator in Phase 2.

Figure 2. (a-b) Osprey (*Pandion haliaetus*, L., 1758) model being flown over pumpkinseed nest during experimental trials. (c) Snell's window view of osprey flying above substrate at site of experiments. (d) Pumpkinseed fanning eggs with tail. (e) Pumpkinseed showing metabolic fright response and dorsal spine erection after introduction of the osprey model overhead. (f) A sneaker-male (pictured left) enters nest of male pumpkinseed (right) in Phase 3 after the animal had been exposed to the osprey. This is a rare scenario that shows the consequences of poor nest defense resulting from exposure to risk effects.

Figure 3. Fish behavioral responses during phase 2 of the experiment: (a) Trips outside the nest, (b) burst swimming bouts, and (c) dorsal spine erections/flares. Red bars represent predator-exposed fish ($n = 21$), blue bars represent control (absence of predator; $n = 17$). Values are presented as mean $\pm$ 1 s.e.m. Statistically significant differences between predator- and control-exposed fish are represented by * ($p < 0.05$).

Figure 4. Changes in fish behaviors between phase 1 and phase 3 of the experiment: (a) rotations in the nest, (b) nest maintenance behaviors, (c) dorsal spine erections/flares, and (d) time spent outside the nest in seconds. Red bars represent predator-exposed fish ($n = 21$), blue bars represent control (absence of predator; $n = 17$). Values are presented as mean $\pm$ 1 s.e.m. Statistically significant differences between predator- and control-exposed fish are represented by * ($p < 0.05$).

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Table 1. Parameter estimates of the ANCOVAs used to test the change in selected behaviors of male pumpkinseed (*Lepomis gibbosus*, L., 1758) exposed to the osprey (*Pandion haliaetus*, L., 1758) predator treatment (predator presence vs. absence/control). The variables body size (cm) and egg score (1-5, from low to high) were used as covariates in the assessment of behavioral change for the pumpkinseed. *** (P<0.001) denote statistically significant effects of the treatment on the individual parameter. Non-significant results (P>0.05) are indicated by “ns”.

Table 1.

Behaviour		SS	DF	MS	F	P	
<i>Rotations in nest</i>							
	Treatment	3008.86	1	3008.86	70.78	0.000	***
	<u>Covariates</u>						
	Body size	2.82	1	2.82	0.07	0.775	ns
	Egg score	3.53	1	3.53	0.08	0.798	ns
	Error	1445.33	34				
<i>Nest attention</i>							
	Treatment	1861.51	1	1861.51	29.31	0.000	***
	<u>Covariates</u>						
	Body size	206.17	1	206.17	3.25	0.080	ns
	Egg score	24.35	1	24.35	0.38	0.540	ns
	Error	2159.32	34	63.51			
<i>Total time outside nest</i>							
	Treatment	1237.28	1	1237.28	15.397	0.000	***
	<u>Covariates</u>						
	Body size	332.32	1	332.32	4.14	0.050	ns
	Egg score	53.09	1	53.09	0.66	0.422	ns
	Error	2732.10	34	80.36			
<i>Dorsal flares</i>							
	Treatment	1127.32	1	1127.32	12.25	0.001	***
	<u>Covariates</u>						
	Body size	40.64	1	40.64	0.44	0.511	ns
	Egg score	75.47	1	75.47	0.82	0.371	ns
	Error	3127.89	34	92.00			
<i>Attacks</i>							
	Treatment	166.59	1	166.59	1.49	0.232	ns
	<u>Covariates</u>						
	Body size	20.16	1	20.16	0.18	0.674	ns
	Egg score	10.95	1	10.95	0.10	0.757	ns
	Error	3588.46	32	112.14			