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ARTICLE

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

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Abstract: The nonconsumptive 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 because the most common fright response 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 nonconsumptive effects of avian predators on parental care in pumpkinseed (*Lepomis gibbosus* (L., 1758)) through 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.

Key words: landscape of fear, *Lepomis gibbosus*, Osprey, *Pandion haliaetus*, parental care, predator, predation risk, pumpkinseed.

Résumé : Les conséquences autres que la consommation des prédateurs sur le comportement, la survie et la démographie des proies ont récemment fait l'objet de beaucoup d'attention de la part d'écologistes. Les impacts des prédateurs de niveau trophique supérieur sur les proies en liberté sont toutefois difficiles à évaluer puisque la réaction de peur la plus répandue des proies consiste à quitter la zone du risque. En outre, il est surprenant de constater le peu de cas fait des impacts descendants des prédateurs aviaires sur les milieux aquatiques. Nous avons étudié les effets autres que la consommation de prédateurs aviaires sur le soin des alevins par les crapets-soleil (*Lepomis gibbosus* (L., 1758)) en utilisant un modèle réaliste d'oiseau prédateur, le balbuzard pêcheur (*Pandion haliaetus* (L., 1758)). Notre prédateur modèle a produit d'importantes réactions métaboliques de peur et des mécanismes de défense inductibles chez les poissons expérimentaux, qui se traduisaient par des changements significatifs dans les comportements de soin des alevins. Les principaux comportements parentaux, dont les rotations au nid et l'entretien des œufs et du nid, étaient clairement modifiés par l'exposition au prédateur, ces variations de la performance parentale pouvant atteindre plus d'un ordre de grandeur, ce qui donne à penser que même un risque de prédation passager peut réduire l'aptitude de reproduction. Nos données fournissent d'importants nouveaux renseignements sur le fonctionnement du paysage de la peur le long de l'interface air–eau et donnent à penser que les prédateurs aviaires pourraient exercer de plus importants effets de contrôle sur les populations de poissons que ce qui était admis auparavant. [Traduit par la Rédaction]

Mots-clés : paysage de la peur; *Lepomis gibbosus*, balbuzard pêcheur, *Pandion haliaetus*, soin des alevins, prédateur, risque de prédation, crapet-soleil.

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). Although 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 because they can represent a broader portion of the total effect predators have on prey (Creel and Christianson 2008).

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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. 1983), 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.

Although many terrestrial and avian predators kill and consume aquatic prey (e.g., Dalton et al. 2009), the nonconsumptive effects of these interactions remain relatively understudied, particularly for large bird predators (Fauchald and Erikstad 2002; Steinmetz et al. 2003; Zydelis 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 (*Lepomis gibbosus* (L., 1758)), a common prey for Osprey throughout their range (Häkkinen 1978; Steeger et al. 1992; Francour and Thibault 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) because guarding males (*i*) do not forage or leave the nest site except under extreme duress and (*ii*) 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 pumpkinseed at this site, we focused our efforts on Osprey and pumpkinseed. Osprey preferentially forage on pumpkinseed in littoral zones of the lake, and the number of active Osprey nests there have ranged from 5 to 10 per year since 2001 (Queen's University Biological Station (QUBS) staff, personal communication).

Experimental design

Field observations occurred along a shallow gravel/sand bar (~500 m long × 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 the hours of 1000 and 1400 under calm and sunny conditions. The depth of the sandbar ranged from 1 to 2 m, and the nesting substrate throughout this region was primarily composed 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 two) and were marked with a white PVC identification tag (10 cm × 5 cm) on the outer rim. The total length (TL) of parental male pumpkinseed was estimated in situ by researchers, as precise measurements of fish size were not possible without capture and thereby resulting in 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 (class 1 = small (120–140 mm); class 2 = medium (140–160 mm); class 3 = large (>160 mm)) and the relative size of each overall egg mass was scored by the same snorkeling team (classes 1–5, where class 1 = very few and class 5 = very many). All nests that we used contained an adult male and egg mass of unhatched, fertilized eggs (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 s 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 (*Lepomis macrochirus* Rafinesque, 1810) (an active nest predator; 100–140 mm total length) housed inside a clear glass container (volume ~4 L) on the edge of the nest for 60 s. 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+; Struthers et al. 2015) and recorded fish behavior continuously for a period of 12 min. This 12 min period consisted of three phases: (1) pre-stimulus, 5 min; (2) stimulus phase (presence/absence of predator model), 2 min; (3) post-stimulus, 5 min (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 (*i*) cumulative time outside the nest (seconds), (*ii*) number of full (360°) in-nest rotations, (*iii*) total number of spinal flares (defined as the erection of dorsal spines), (*iv*) number of burst behaviors (defined as rapid, erratic swimming behaviors across the nest), and (*v*) 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 mean duration from when the predator was introduced until the 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 those that never returned.

Predator simulation

Predator models used in phase 2 comprised an artificial Osprey kite (112 cm wingspan, 45 cm head to tail; Jackite Inc., Virginia Beach, Virginia, USA) attached to a 6 m telescopic pole by way of a 1 m string (Fig. 2*a*). The model bird mimicked the colors, patterns, shape, and realistic flying manner (gliding and swooping behavior) of Ospreys. At the onset of phase 2, a trained snorkeler slowly

Fig. 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*), broken down by the three phases of each experimental trial. White dishes represent nests. Controls did not receive a predator in phase 2. Figure appears in color on the Web.

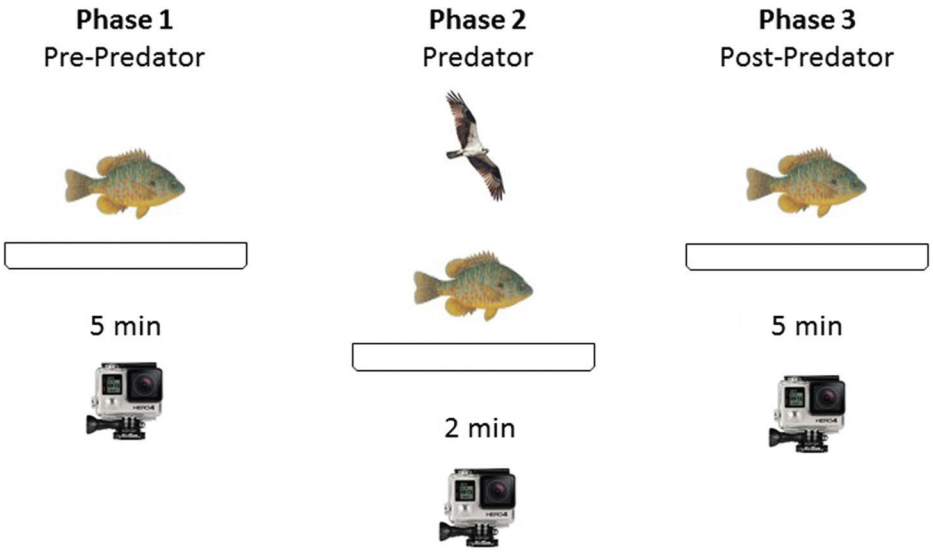
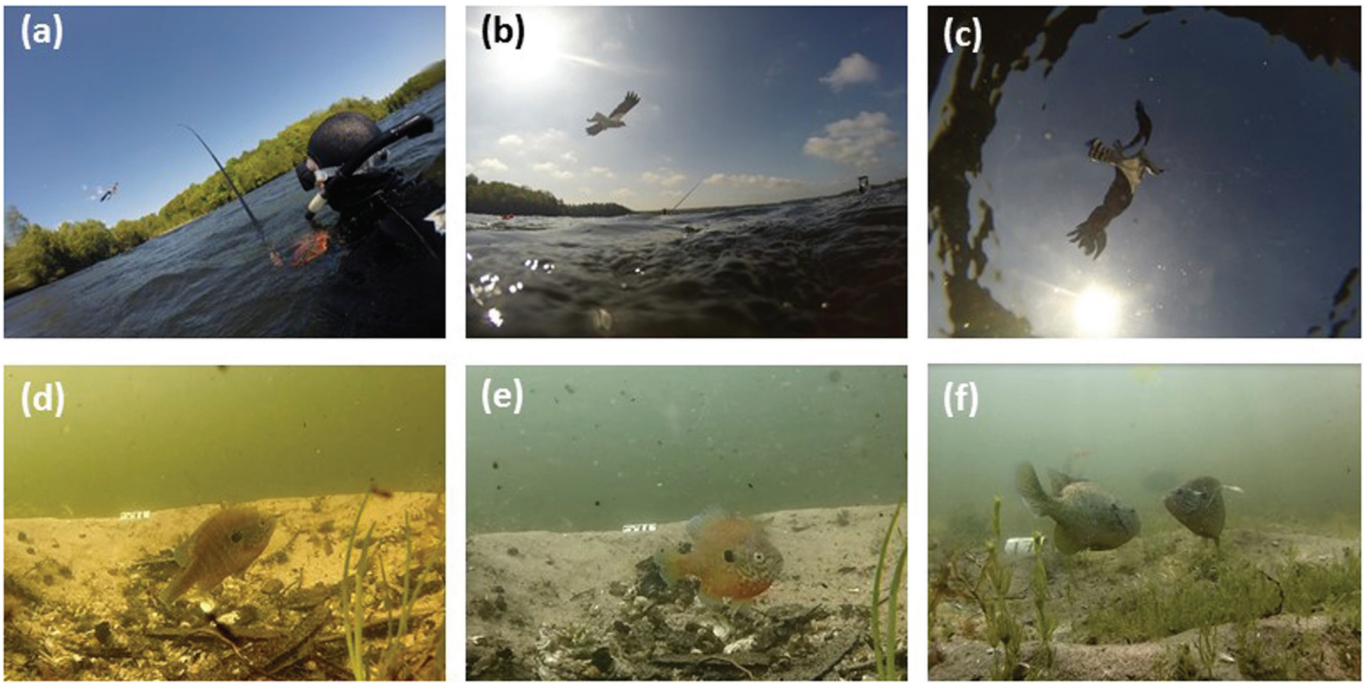


Fig. 2. (*a–b*) Osprey (*Pandion haliaetus*) model being flown over pumpkinseed (*Lepomis gibbosus*) nest during experimental trials. (*c*) Snell's window view of Osprey flying above substrate at site of experiments. (*d*) Pumpkinseed fanning eggs with tail. (*e*) Pumpkinseed showing metabolic fright response and dorsal spine erection after introduction of the Osprey model overhead. (*f*) A sneaker male (pictured left) enters nest of male pumpkinseed (pictured 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 appears in color on the Web.



approached the nest from offshore until the Osprey kite was positioned above the center of the nest (Fig. 2*b*; about 6 m away to minimize observer bias). For a period of 2 min, we flew the Osprey over the nest, using gentle movements to move the bird laterally and vertically (~2 m above the nest; Fig. 2*c*). We chose this height because it is a realistic simulation of how Osprey hunt fish from above. After the final 5 min 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 s.

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 in the other treatment and snorkelers maintained a minimum distance of 3 m 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 (species of the genus *Micropterus* Lacepède, 1802) 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 Student's *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 phases 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 phases 1 and 3). All data were 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, they were compared between treatments (predator presence/absence) using a one-way multivariate analysis of variance (MANOVA). Subsequent analysis of covariance (ANCOVA) was run on each behavior/dependent variable to contrast mean behavioral ranks between treatments using estimated fish size and egg score as covariates. To promote context and relevance to behaviorally meaningful information, all graphical plots present nontransformed data. All statistical analyses were conducted in SPSS at $p < 0.05$ level of significance. Values are presented as mean ± 1 SE unless otherwise indicated.

Results

Thirty-eight trials (predator stimulus, $n = 21$; predator absence, $n = 17$) were conducted that resulted in a total of 456 min of video footage used for behavioral quantification and analysis. The mean (±1 SE) fish latency to respond to the model was 7.9 ± 1.5 s. 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 ($p < 0.001$; Figs. 3*a*–3*c*). The before-and-after behavior of nesting male pumpkinseed was also significantly affected by the experimental predator treatments (MANOVA, $F_{[1,34]} = 17.70$, $p < 0.0001$; Figs. 4*a*–4*d*). Four of the five variables that 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, on average, 9.76 ± 1.37 fewer rotations after being exposed to the predator cues, which is an order of magnitude fewer than when the cues were absent (Fig. 4*a*). Fish exposed to predator cues also showed, on average, 5.05 ± 1.03 lower nest maintenance behaviors when compared with a slight positive change of 0.18 ± 0.47 nest maintenance behaviors when the fish were not exposed to predator cues (nearly five times fewer; Fig. 4*b*).

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. 4*c*). Predator-exposed fish also spent, on average, around 60 times more time (in seconds) outside the nest relative to controls (Fig. 4*d*). 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

Fig. 3. Pumpkinseed (*Lepomis gibbosus*) behavioral responses during phase 2 of the experiment: (*a*) trips outside the nest, (*b*) burst swimming bouts, and (*c*) dorsal spine erections/flares. Pale red bars (gray bars in print) represent predator-exposed fish ($n = 21$), whereas blue bars (dark gray bars in print) represent control (absence of predator; $n = 17$). Values are presented as mean ± 1 SE. Statistically significant differences between predator- and control-exposed fish are represented by an asterisk (*, $p < 0.05$). Figure appears in color on the Web.

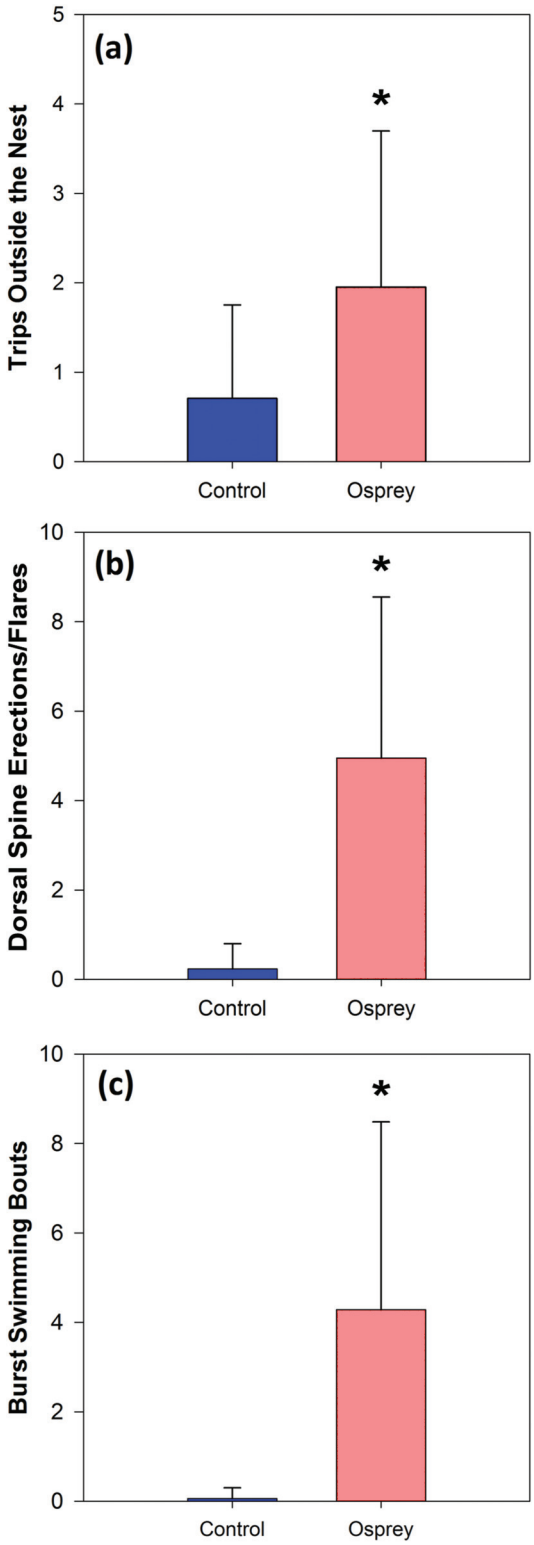
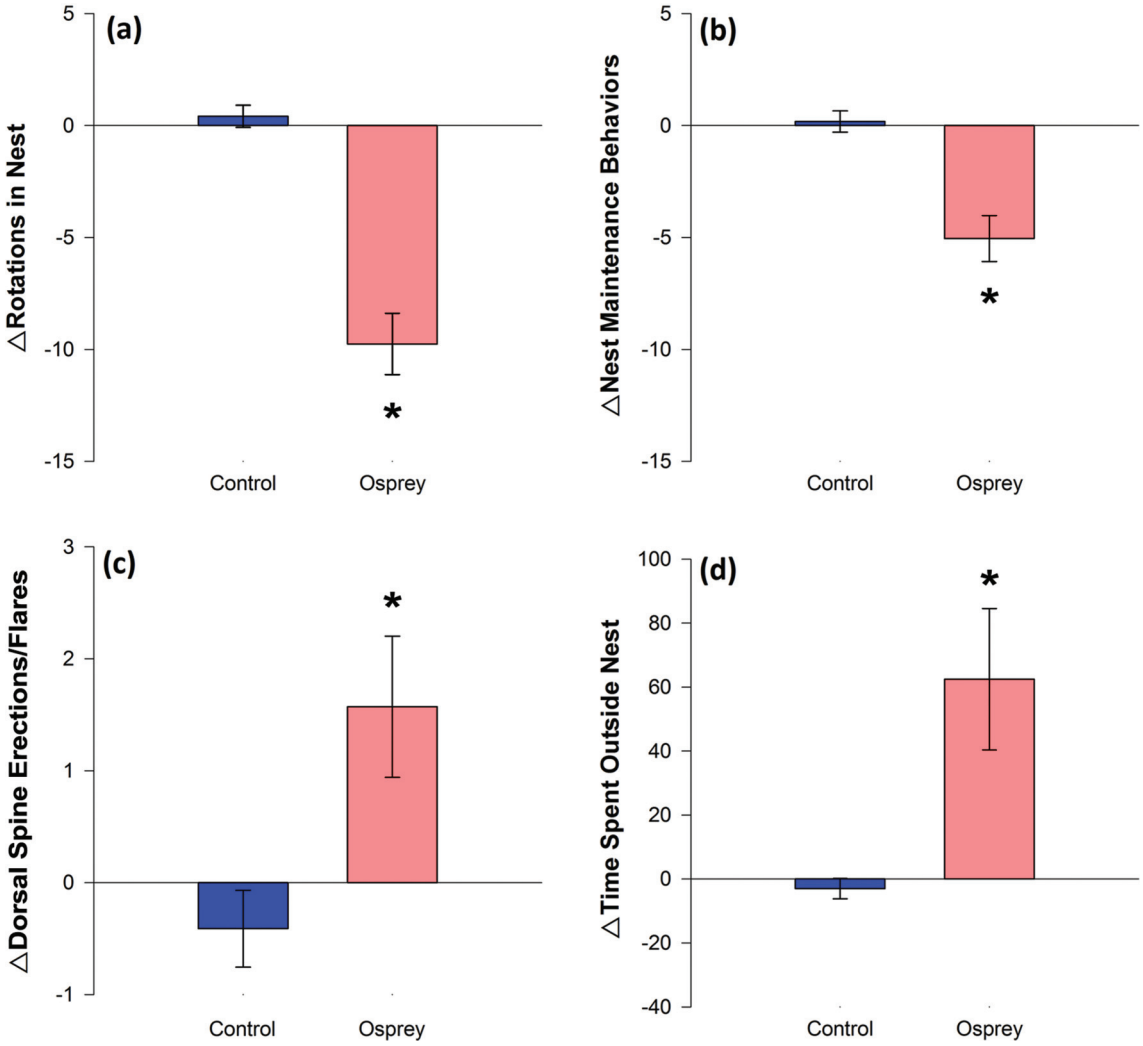


Fig. 4. Changes in pumpkinseed (*Lepomis gibbosus*) behaviors between phase 1 and phase 3 of the experiment: (*a*) rotations in the nest, (*b*) nest maintenance behaviors, (*c*) dorsal spine erections/flares, and (*d*) time spent outside the nest in seconds. Pale red bars (gray bars in print) represent predator-exposed fish (n = 21), whereas blue bars (dark gray bars in print) represent control (absence of predator; n = 17). Values are presented as mean ± 1 SE. Statistically significant differences between predator- and control-exposed fish are represented by an asterisk (*, $p < 0.05$). Figure appears in color on the Web.



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 s) 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, as well as 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, that mediates a host of physiological scale effects including energy mobilization, cardiovascular activity, and protein synthesis; an essential process that works to mitigate the negative impacts of the stressor (reviewed in Barton 2002). Physiological effects of both cortisol and catecholamine secretions, under a predation threat, are likely to be mediating the behavioral responses observed here (Hawlena 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 (Figs. 3*a*–3*c*). Dorsal spines have evolved in fishes as a predator-deterrence mechanism reducing prey susceptibility and foraging profitability by the predator (Huntingford et al. 1994). 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 that occurred throughout the nest when the predator was overhead, and that occurred nearly four times more under the threat of predation (Fig. 3*b*) 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, 2011). Fish also increased their trips outside the nest under the threat of predation (Fig. 3*c*), presumably showing that the risk of mortality outside the nest is lower than when a

Table 1. Parameter estimates of the ANCOVAs used to test the change in selected behaviors of male pumpkinseed (*Lepomis gibbosus*) exposed to the Osprey (*Pandion haliaetus*) predator treatment (predator presence vs. absence/control).

Behavior	Statistic	SS	df	MS	*F*	*p*
Rotations in nest	Treatment	3008.86	1	3008.86	70.78	**0.000*****
	Covariates					
	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			
Nest attention	Treatment	1861.51	1	1861.51	29.31	**0.000*****
	Covariates					
	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		
Total time outside nest	Treatment	1237.28	1	1237.28	15.397	**0.000*****
	Covariates					
	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		
Dorsal flares	Treatment	1127.32	1	1127.32	12.25	**0.001*****
	Covariates					
	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		
Attacks	Treatment	166.59	1	166.59	1.49	0.232 ns
	Covariates					
	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		

Note: 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. A triple asterisk (***, $P < 0.001$) denotes statistically significant effects of the treatment on the individual parameter. ns indicates nonsignificant results ($P > 0.05$). SS, sum of squares; df, degrees of freedom; MS, mean squares.

predatory bird is circling overhead (indeed, the fish shape is strongly contrasted against the excavated nests). By exposing largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) 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 nonlethal 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 tradeoffs because 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 five times lower nest-related maintenance behaviors under predation risk (Figs. 4*a*, 4*b*). In-nest rotations and nest maintenance (fanning of eggs, cleaning of nest) are the two most common behaviors exhibited by parental pumpkinseed (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, on average, ~3 rotations/min, which dropped by above 50% under predation risk. 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 that we observed in nest-maintenance behaviors (Fig. 4*b*), including significant decreases in nest-maintenance behavior such as fanning (Fig. 2*c*), which promote oxygen transfer to eggs as they develop, and time spent outside the nest (Fig. 4*d*), 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 that 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 that they may be appreciable).

Studies of predation risk on nesting birds have demonstrated that "intimidating" prey species through nonlethal 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). Although 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 that 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 behavior and survival (Hill and Heck 2015; Pepino et al. 2015).

By showing how, behaviorally, avian predators affect prey in a nonconsumptive 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; (2) the recovery of avian predators can restore an essential ecosystem service, i.e., predation risk. Ospreys are one of the greatest examples of conservation success in North America because 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 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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