Ethology

Influence of Inter-Lake Variation in Natural Nest Predation Pressure on the Parental Care Behaviour of Smallmouth Bass (*Micropterus dolomieu*)

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Received: January 19, 2009
Initial acceptance: January 23, 2009
Final acceptance: January 29, 2009
(L. Ebensperger)

doi: 10.1111/j.1439-0310.2009.01641.x

Abstract

Predation risk has the ability to greatly influence the behaviour of reproducing individuals. In large long-lived species with low risk of predation for parents, reproductive behaviours often involve caring for offspring (i.e. defending broods from predators) and these behaviours are essential for offspring survival. Our objectives were to test for the presence of natural variation in nest predation pressure in an aquatic environment for a species that provides sole-paternal care, smallmouth bass (*Micropterus dolomieu*), and to determine if natural variation in predation pressure influences parental care behaviour. We used snorkeler observations and a series of metrics to assess predation pressure and parental care behaviour in six lakes within a narrow geographical range. Lakes differed in all predation pressure metrics: number of predators in proximity to nest when males were present, time to predator arrival and number of predators that consumed eggs when males were absent and total number of nests that was preyed upon. Similarly, parental behaviour varied between lakes. Parental smallmouth bass spent more time engaged in anti-predator defences in lakes with high predation pressure, while males from low predator pressure lakes remained close to their nest. Conversely, males from lakes with low and high predation pressure showed a similar willingness to defend their nests during simulated nest predation events. Our results show that natural variation in aquatic nest predation pressure across multiple lakes can be significant and has the ability to influence baseline parental care behaviour. Such variation provides opportunities to study the costs and consequences of parental care and to evaluate how this could influence demography and community interactions in aquatic systems.

Introduction

Predation is often considered one of the greatest potential costs of reproduction (Magnhagen 1991). Reproducing animals can be physically impaired during reproduction (e.g. pregnancy, ornamentation), but it is generally their reproductive behaviour such as mate searching, mate signalling or mate calling which makes them more vulnerable to predation (reviewed by Lima & Dill 1990). Indeed, much literature has focused on how predators use the olfactory, auditory and visual cues of reproducing individuals to increase prey detection (reviewed by Zuk & Kolluru 1998). As a result, a wide range of studies have sought to describe the behavioural adjustments made by individuals to cope with the trade-offs that exist between reproductive success and predator avoidance [e.g. intersexual response to auditory predator cues in frogs (Bernal et al. 2007); predation pressure affects mate choice in colourful fish (Forsgren 1992; Gong & Gibson 1996)].

Alternatively, predation can have little effect on the survival of reproducing individuals, but an important effect on the survival of the developing offspring. In large, long-lived species that provide parental care and have low risk of individual predation, efforts are devoted to caring for offspring (e.g. defending broods from predators). Based on the level of parental investment, these behaviours can be rather costly and include a suite of potential consequences such as loss of mass (Townsend 1986; Moreno 1989), depletion of energy stores (Steinhart et al. 2005) and reduced future breeding opportunities (Coleman et al. 1985). In this case, the interactions with potential brood predators do not directly influence parent survival, but has the potential to influence the costs and consequences of providing care. Avian ecologists have long been interested in how predation pressure affects clutch size (e.g. Slagsvold 1984; Doligez & Clobert 2003), and have more recently examined how parental behaviour may influence offspring survival. There is strong evidence that an increase in parental care activities such as the feeding of nestlings or incubating female can increase nest predation rates (Martin et al. 2000). In addition, birds will reduce their nest visitation rates (Ghalambor & Martin 2002), become more cryptic or reduce clutch size (Eggers et al. 2006) when nest predation pressure is elevated.

Contrary to birds, there is little evidence that the parental care activities of fish are used as cues by nest predators. As such, fish seem to have evolved different optimal strategies as a response to changes in predation pressure and will often become more aggressive (Ridgway 1988; Ongarato & Snucins 1993) or increase their individual risk taking (Magnhagen & Vestergaard 1991) when nest predation pressures increase. This, in addition to fundamental ecological differences between birds and fish, make fish an interesting model to examine the influence of offspring predation pressure on the costs and consequences of parental care (Amundsen 2003). For example, by providing offspring with food and warmth, birds (and other animals) provide a form of depreciable parental care, where the individual offspring benefits decrease as the brood size increases. Conversely, the most common type of care in fish is guarding eggs or developing offspring from potential predators (Gross & Sargent 1985), a form of undepreciable care (Clutton-Brock 1991). Other ecological differences such as growth rate, survival, egg characteristics (size and number) and the abundance of aquatic predators, seem to make fish more susceptible to nest predation than birds (Magnhagen 1992), thus making fish particularly interesting to evaluate the differential effects of nest predators.

Here, we use the smallmouth bass (*Micropterus dolomieu*; teleostei: centrachidae) as a model to evaluate the effects of variation in natural nest predation pressure across six lakes within a narrow geographical range. In this species, adults are often the top predator in the system and have low risk of adult predation besides threats imposed by anglers or the occasional bird of prey (Scott & Crossman 1973). Males provide sole parental care for up to 6 wk (Ridgway 1988), where they perform energetically costly activities (Cooke et al. 2002, 2006) such as egg fanning to provide oxygen and prevent silt deposition, as well as brood defence. Similar to other animals, parental smallmouth bass perform a limited suite of nesting behaviours. They may be away from their nest (performing other behaviours such as foraging), on or near their nest (tending their eggs by fanning or vigilance) or actively chasing away nest predators (Ridgway 1988). If a smallmouth bass leaves his nest unattended for a short period of time, brood predation may occur (Kieffer et al. 1995; Philipp et al. 1997; Steinhart et al. 2004). In addition, smallmouth bass will actively and aggressively defend their nest from natural and model nest predators (Ridgway 1989; Urban 1991). The native range of smallmouth bass encompasses much of eastern and central North America (Scott & Crossman 1973) and thus includes a wide range of natural variation in environmental conditions, including predation pressure (Hinch & Collins 1991; Steinhart et al. 2005). A previous study has evaluated the interspecific variation of nest predation pressure within a single lake among six syntopic centrachid fishes (including smallmouth bass; Cooke et al. 2008), and between two lakes with and without an invasive nest predator (Steinhart et al. 2005). However, little is known about the natural variation in nest predation pressure among populations and if such variation influences the costs and consequences of parental care. Such information could provide insight into the extent of intraspecific variation in organismal behaviour and its ecological and evolutionary basis.

As such, our goal was to examine how natural variation in nest predation pressure influences parental care behaviour in smallmouth bass. We tested for the presence of variation in nest predation pressure across six lakes within a narrow geographic range where other environmental variables (e.g. climate drivers) would presumably be similar. Once the predation pressure gradient was established, we tested two hypotheses. First, we hypothesized that 'baseline' parental care behaviour would be influenced by nest predation pressure. We predicted that smallmouth bass in lakes with high predation pressure would spend more time on their nest and engaged in anti-predator responses than fish in low predation pressure lakes. Second, we hypothesized that 'elicited' anti-predator responses would not be influenced by predation pressure. Because the fitness consequences of allowing a nest predator to consume ones offspring are so great, we expected nesting males to recognize a nest predator and actively defend his nest from the intrusion irrespective of the population level of predation pressure. Collectively, this study will provide the first data on the variation in natural nest predation pressures across multiple lakes and the consequences of such variation on parental care behaviour. Such studies are urgently needed to understand the interface between community ecology and individual behaviour, yielding a more mechanistic ecology and predictive ethology (Altmann & Altmann 2003).

Methods

Study Area

Smallmouth bass were studied in six lakes in the spring of 2007 (<50 km between most distant lakes) within the same ecoregion in southeastern Ontario (Big Rideau Lake, Charleston Lake, Indian Lake, Newboro Lake, Opinicon Lake and Sand Lake). The last smallmouth bass stocked in Ontario was in 2000 and hatchery production (at the provincial level) has been negligible since the 1930s, hence there should be minimal influence from supplementation (Kerr 2006).

In the spring when temperatures reach approx. 15°C, male bass move into the littoral zone where they sweep out a nest in the substrate with their caudal fin, court females, spawn, and then provide parental care to the brood until the offspring become independent. Because of the ecological differences between lakes such as depth and turbidity, lakes warm differentially and allow for temporal variation during the reproductive season. Peak spawning dates, even within a small geographic region such as southeastern Ontario, can vary by approx. 10 d (Kubacki et al. 2002) enabling research to take place in multiple lakes within a small geographic area in a single season. Lakes were chosen because of their proximity to each other (less than 50 km) and the indication that they showed inherent variation in nest predation pressure (based on interviews of biologists with the Ontario Ministry of Natural Resources and local sunfish researchers, Frank Phelan and David Philipp). As the reproductive season began, snorkelers swam a subset of the littoral zone of each lake to identify the location of approx. 30 nesting males on eggs (≤ 4 d). Distances swam in each lake ranged approx. between 1 and 3 km. Snorkelers estimated the egg score (ES) in each nest [a categorical metric from a low of 1 to a high of 5 (Kubacki et al. 2002)] and age of eggs (fresh eggs are golden with a visible oil droplet and gradually whiten within a few days). Factors such as male size, number and age of eggs are known to affect the behaviour of nest guarding males (Ridgway 1988, 1989; Suski et al. 2003) and were considered in analyses. Individual nests were identified with a numbered marker. Study sites within a lake were selected based upon previous research by our team or colleagues and focused on areas with appropriate spawning substrate (i.e. coble and gravel). All sampling occurred from May to June 2007. All observations were collected at the egg stage when predation pressure can be quite high because fresh eggs are energetically valuable to predators and can be easily captured because they are immobile.

Lake Predation Pressure

We used several metrics to establish the level of nest predation pressure in the six lakes. All observations were made by a snorkeler and were recorded on dive-slates. The first metric directly quantified the predation pressure of each smallmouth bass nest. This study was performed in conjunction with others (M.-A.Gravel, unpubl. data) which required relocating unmanipulated individuals at a later date. For this reason, only a proportion of individuals were used in this study. To select individuals, one in every three nests were chosen along transects swam by snorkelers. Overall, 10 smallmouth bass nests were chosen from the nests previously marked by the snorkeler and were observed for 15 min with the snorkeler positioned 3 m from the nest. There was a short 1–2 min acclimation period but typically this distance was sufficient in preventing the disturbance of normal parental care behaviour. Only five of 59 fish reacted to the snorkeler and were removed from the baseline behaviour analysis. At 30 s intervals, the snorkeler recorded the number and species of nest predators that were within 2 m of the nest. The maximum number of predators within the 15-min period was determined for each nest because individual predators could not be identified and reporting means would be ambiguous. We considered fish to be potential nest predators if they had been previously reported as being such for bass nests in the literature or if we had observed them doing so. For the purpose of this study that list included bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), yellow perch (*Perca flavescens*), black crappie (*Pomoxis nigromaculatus*), largemouth bass (<15 cm) (*Micropterus salmoides*) and conspecifics (<15 cm). The 2 m distance was chosen to ensure the same amount of visibility across all lakes. Moreover, previous studies of smallmouth bass have revealed that bass actively defend against predators within 2 m of the nest (e.g. Cooke et al. 2008). After the conclusion of the 15-min observation period, the fish was removed from the nest by rod and reel. The snorkeler observed the nest area for an additional 15-min period and noted the time elapsed between the removal of the parent and the arrival of the first nest predator. At each 1 min interval, the snorkeler would also note the number and species of nest predators present and engaged in consumption of eggs at the abandoned nest.

Baseline Parental Care

Baseline parental care was measured during the initial 15-min sampling time and on the same 10 randomly sampled fish described above. At 30 s intervals, the snorkeler noted the activity being performed by the guarding male. Activity was a categorical measurement and fish could be performing only one activity at each time interval: (1) away from nest (>2 m from nest) and/or not visible to the snorkeler; (2) on nest or within 2 m of nest; or (3) engaged in an anti-predator behaviour.

Elicited Anti-Predator Response

Prior to the removal of nesting males, anti-predator behaviours were elicited using a predatory sunfish (*Lepomis* spp.) (mean total length (TL) ± SE; 149.25 ± 7.54 mm) placed in a glass jar. Smallmouth bass display three types of aggressive behaviours when encountering nest predators: yawn (males open their mouths and flare their branchiostegal membranes), rush (males quickly swim towards predator but do not strike) and hit (males make physical contact with the predator by striking or biting) (Suski et al. 2003). To elicit an anti-predator response, the nest predator was placed 1 m from the nest for 30 s and then placed within the nest for 30 s. During this time, the snorkeler counted the number and type of aggressive behaviours made by the male towards the nest predator. The effect of distance was identical for all males across all lakes (data not shown), thus anti-predator behaviours for both distances were summed for statistical analysis.

Statistical Analysis

All analyses were performed in JMP 7.0.1 (SAS Institute Inc, Cary, NC, USA) and the level of significance (α) for all tests was 0.05. All figures display $\bar{x} \pm$ SE unless otherwise indicated. One-way ANOVAS were used to test for differences between the six lakes for each response variable (predation pressure metrics and staged intrusion) and for other traits that may have influenced predation pressure and/or parental behaviour such as male TL, ES and egg age. Data were tested for normality and heterogeneity of variance prior to analyses. Most response variables could not be transformed to fit the normal distribution and thus a non-parametric Kruskal–Wallis test was performed. These analyses were then followed by parametric or non-parametric multiple comparisons, respectively (Zar 1999). We used a univariate time-to-event (survival) analysis to test for differences in time to depredation as some nests were never preyed upon and data needed to be censored (i.e. censorship in a time-to-event analysis takes into consideration that the event did not occur within the given observation time). We used a 6 × 3 contingency table to compare the time spent performing each baseline behaviour and the number of nest with difference ESs across the six lakes. We then examined the standardized residuals from the behavioural analysis [$R = (F_0 - F_e)/\sqrt{F_e}$] to determine which cells, if any, had a major influence ($-1.96 \geq R \geq 1.96$) on significance (Haberman 1973).

Results

Male Size, Egg Score and Egg Age

Nesting smallmouth bass did not differ in TL between lakes ($F_{5,53} = 0.9$, $p = 0.48$) (range: 394–497 mm; $\bar{x} \pm$ SE: 408.3 ± 5.7 cm). ES categories ranged from 2 to 4 and differed between lakes (Kruskal–Wallis, $\chi^2 = 12.2$, df = 5, $p = 0.03$) (Fig. 1).

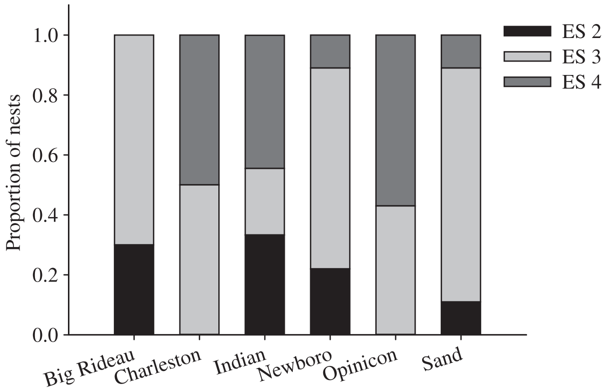

Fig. 1: Proportion of nests with different egg scores (ES) within each lake.

Egg age did not differ between lakes (Kruskal–Wallis, $\chi^2 = 5.4$, df = 5, p = 0.37). Variation in ES did not affect the number of predators in proximity to the nest in the presence of males (Kruskal–Wallis, $\chi^2 = 2.4$, df = 5, p = 0.30) or the level of aggression of males during a staged nest predator invasion ($F_{5,51} = 0.65$, p = 0.53).

Nest Predation Pressure

Potential and actual nest predators documented in this study were bluegill, pumpkinseed and rock bass. Over 95% of predators identified in all observations were *Lepomis* spp. and thus individual predator species effects were not included in analyses and all predator species were grouped. The number of nest predators in proximity to a nest in the presence of a guarding male (perceived predator abundance) varied across lakes (Kruskal–Wallis, $\chi^2 = 23.1$, df = 5, p = 0.0003; Fig. 2a). Here, Sand Lake and Opinicon Lake had the highest perceived predation pressure, while Big Rideau Lake had the lowest. Similarly, time to depredation (time-to-event analysis, $\chi^2 = 25.6$, df = 5, p = 0.0001) and the proportion of nests which were preyed upon were also influenced by lake (Fig. 3). By the first minute, 60% of nests from Opinicon Lake were attacked by a nest predator, while it took over 5 min for most of the lakes to reach 30% predation. At the end of the 15-min period, Big Rideau Lake had the lowest number of nests preyed upon (3/10) and Opinicon Lake had the greatest number of nests that were attacked by predators (9/10). The number of predators present after male removal (actual predation pressure) also differed between lakes (Kruskal–Wallis, $\chi^2 = 13.7$, df = 5, p = 0.02; Fig. 2b). Opinicon Lake had the greatest number of predators arrive after removal, while Big Rideau Lake had the lowest.

Parental Care Behaviour

The proportion of time spent performing baseline parental behaviours differed between lakes ($\chi^2 = 83.9$, df = 10, $p < 0.0001$; Fig. 4). Males from Opinicon Lake were most often engaged (11%) in anti-predator behaviours. Residuals from the contingency analysis (Table 1) revealed that time spent away from nest in Big Rideau Lake and Opinicon Lake and time engaged in anti-predator activities from Opinicon Lake were significantly over-represented in the sample, while time spent engaged in anti-predator activities were significantly under-represented in Big Rideau Lake and Charleston Lake

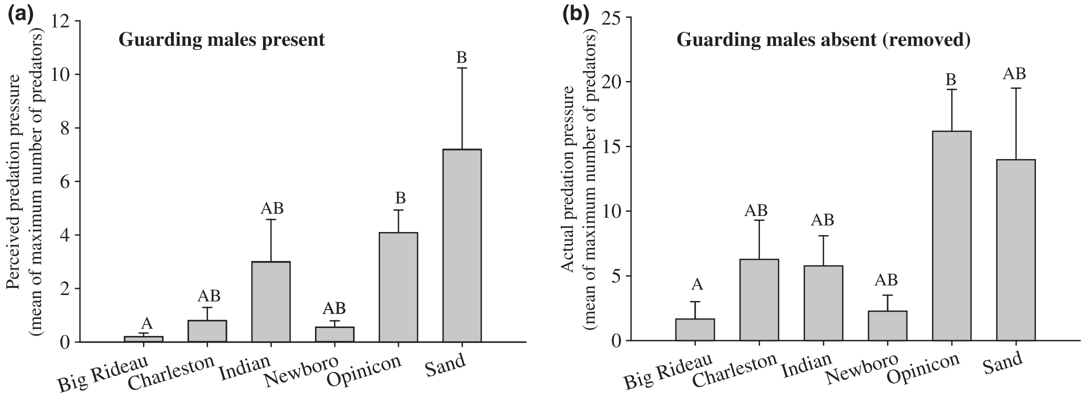

Fig. 2: (a) Perceived predation pressure, guarding male present and (b) actual predation pressure, guarding male absent (removed) in six lakes ≤50 km radius in SE Ontario (Big Rideau Lake, n = 10; Charleston Lake, n = 10; Indian Lake, n = 10; Newboro Lake, n = 9; Opinicon Lake, n = 10; Sand Lake, n = 10). Dissimilar letters denote significant differences between means (Tukey *post hoc* test, $p < 0.05$).

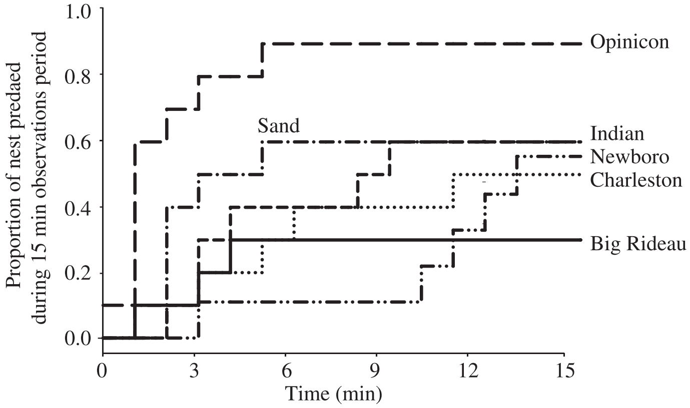

Fig. 3: Time to depredation expressed as proportion of nests preyed upon within a 15-min period following the removal of nest guarding males in six lakes (≤50 km radius) in SE Ontario (Big Rideau Lake, n = 10; Charleston Lake, n = 10; Indian Lake, n = 10; Newboro Lake, n = 9; Opinicon Lake, n = 10; Sand Lake, n = 10).

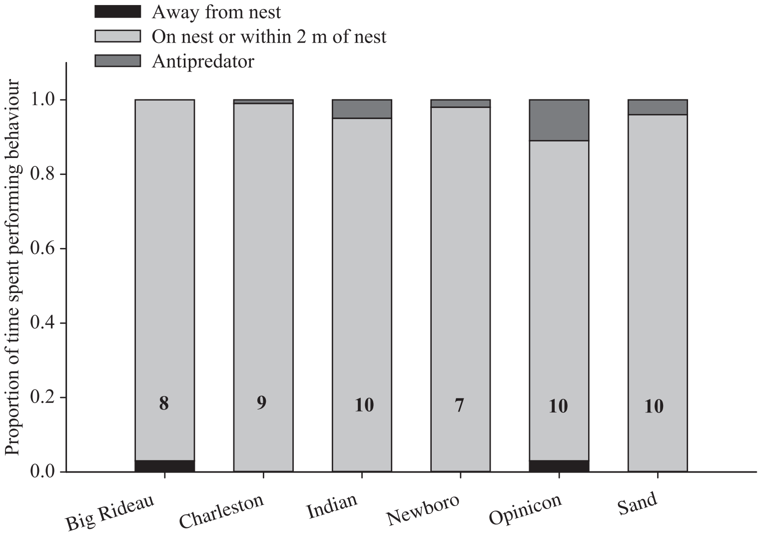

Fig. 4: Proportion of time nest guarding smallmouth bass spent performing distinct parental care behaviours in six lakes (≤ 50 km radius) in SE Ontario. Sample sizes are shown on individual bars.

Table 1: Residuals from 6 × 3 contingency analysis between lakes and baseline parental care behaviour

	Activity		
Lake	1	2	3
Big Rideau	**3.08**	0.31	**−3.16**
Charleston	−1.78	0.66	**−2.15**
Indian	−1.35	0.05	0.70
Newboro	−1.57	0.50	0.70
Opinicon	**2.99**	−1.50	**5.69**
Sand	−1.35	0.17	−0.12

1, away from nest; 2, within 2 m of nest; 3, engaged in an anti-predator behaviour.

Bold-faced residuals are considered significant ($p < 0.05$) if above the standardized residual of +1.96 or below −1.96.

(Table 1). The number of yawns and hits performed by parental males towards a staged nest predator also varied between lakes (yawns; Kruskal–Wallis, $\chi^2 = 18.65$, df = 5, p = 0.002) (hits; $F_{5,53} = 3.6$, p = 0.007), while the number of rushes did not (Kruskal–Wallis, $\chi^2 = 5.1$, df = 5, p = 0.4) (Fig. 5).

Discussion

Predation is considered an intense selective force able to influence the morphology and behaviour of organisms. In addition to its evolutionary importance, it is also relevant on ecological time scales, where organisms make behavioural adjustments in response to predation threats in their own lifetime (reviewed by Lima & Dill 1990). Although manipulative experiments have elucidated the behavioural consequences of predation pressure (e.g. Fontaine & Martin 2006; Eggers et al. 2008), little work has examined the ecological significance of natural variation in predation pressure. This study showed clear evidence for natural variation in nest predation pressure within a narrow geographic range. Lakes were

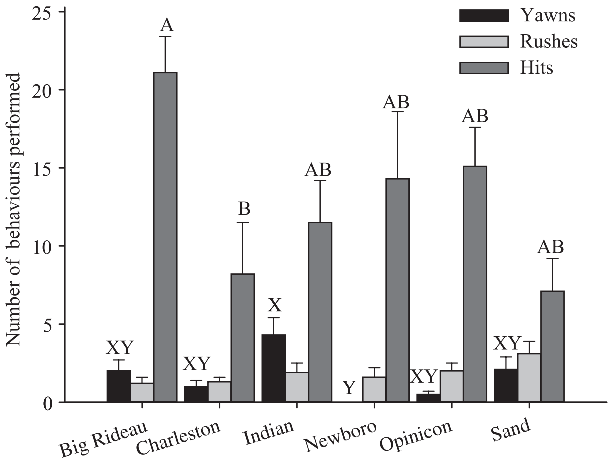

Fig. 5: Mean number of anti-predator behaviours performed by parental smallmouth bass towards a staged nest predator (*Lepomis* spp.) (Big Rideau Lake, n = 10; Charleston Lake, n = 10; Indian Lake, n = 10; Newboro Lake, n = 9; Opinicon Lake, n = 10; Sand Lake, n = 10). Dissimilar letters denote significant differences for a given anti-predator behaviour (Tukey *post hoc* test, $p < 0.05$).

relatively constant in their 'rankings' such that lakes that showed evidence for high predation pressure in one metric, ranked similarly for other metrics. Lakes that were statistically highest in predation pressure metrics were Opinicon Lake and Sand Lake, while Big Rideau Lake was consistently the lowest. Of particular note is the proportion of nests that were preyed upon when parental males were removed. In Opinicon Lake, 90% of nests had eggs eaten by predators while Big Rideau Lake only had 30% (Fig. 3). Hence, the perceived predator abundance in the presence of males (Fig. 2a) was representative of the actual number of nests which would be preyed upon in their absence (Figs 2a and 3).

In addition to this apparent natural variation in nest predation pressure, this study demonstrates behavioural consequences of this natural phenomenon. Time spent performing parental behaviours differed between lakes and these differences were consistent with the nest predation pressure gradient. Our analysis tested whether males from all lakes spent the same amount of time engaged in each form of parental care behaviour. Opinicon Lake, which showed one of the highest means in predation pressure metrics (Fig. 2) had males spend more time engaged in anti-predator behaviours relative to the other lakes (Table 1, Fig. 4). Males from lakes with lower predation pressure such as Big Rideau Lake and Charleston Lake spent significantly less time engaged in anti-predator behaviours than the other lakes (Table 1, Fig. 4). Males from both predation pressure extremes (high, Opinicon Lake and low, Big Rideau Lake) spent more time than expected away from their nests (Table 1). Although these results appear similar, our snorkeling observations enabled us to distinguish between two distinct behaviours. Males from Opinicon Lake were out of snorekeler view because of the performance of anti-predator behaviours (largely chasing), while males from Big Rideau Lake were occasionally further than 2 m from nest but were not engaged in anti-predator behaviours. It is possible that males from Big Rideau Lake may simply be less bold towards snorkelers or other intrusions than males from other lakes because of low predation pressure and high visibility.

Conversely, our predator simulation data does not show evidence of 'shy' individuals in lakes with low predation pressure. Here, parental smallmouth bass from Big Rideau Lake showed similar or even increased willingness to defend against an introduced nest predator than males from other lakes (Fig. 5). As predicted, parental males from all lakes were generally similarly willing to defend their eggs from staged predator intrusion. The significant difference between the number of hits performed by males from Big Rideau Lake and Charleston Lake, both with relatively low predation pressure, was unexpected and is difficult to explain. Males from Big Rideau Lake may simply have more energy and be more able to defend their nest during an intrusion relative to conspecifics in systems with more constant predation pressure. Individuals in environments with higher predation pressure would be more regularly engaged in anti-predator behaviours such as chasing, an energetically demanding event. However, it is currently not possible for us to determine if this is this case with our existing data. What is important to note is that lakes from predation pressure extremes typically grouped together. Moreover, we confirmed that the vast majority of males (57/59) were able to detect and perform anti-predator behaviours during a staged intrusion, independent of nest predation pressure. Males from Big Rideau Lake and Opinicon Lake performed the same amount of anti-predator behaviours during the staged nest intrusion. This work supports other studies that have highlighted the importance of plasticity in the predator response (Ghalambor & Martin 2002) because males from low predation pressure environments are still able to actively defend their nests.

This study has demonstrated the importance of natural variation in nest predation pressure and its potential consequences on parental care behaviour and also provides opportunities for future research into natural variation of nest predation pressure. Recent work has shown that community structure can have significant consequences on physiological indicators of performance in natural systems (Kaufman et al. 2006). This study showed intraspecific variation in top predator (walleye, *Sander vitreus*) enzyme activities in relation to energetically demanding and ecological relevant activities such as prey capture. Another study has highlighted the loss of energy stores and increased energetic in a system with a novel predator (Steinhart et al. 2005). Thus, it is highly probable that fish providing parental care across a natural predator gradient not only demonstrate differential behavioural responses as we report here, but also exhibit associated physiological and energetic responses.

Although the nest predation pressure is believed to be relatively stable in this system (i.e. we used historical data and local knowledge to find lakes with variation in nest predation pressure), we recognize that systematic annual sampling has not yet been performed. As such, there is also opportunity for inter-annual variability in predation pressure which may have behavioural implications. Knowledge of the stability of predation pressure in a system across multiple years would help with understanding the evolutionary basis of anti-predatory behaviour and parental care. Our results suggest that there is potential for important natural variation in nest predation pressure within a narrow geographical range and that natural variation in nest predator can indeed affect the behaviour of parental care providing species. Although it can be powerful to manipulate predation pressure during the reproductive period to test for behavioural adjustments, it is also of interest to examine how individuals respond in a more natural environment. This study is comprehensive as it tests not only for the presence of variation in natural predation pressure, but also examines the effects of this variation on a species whose main goal during reproduction is the protecting of offspring.

Acknowledgements

The authors would like to thank Michelle Caputo, Mike Donaldson, Andrew Gingerich, Kyle Hanson, Sean Landsman, Connie O'Connor, Amanda O'Toole, Rana Sunder and Tara Redpath for their outstanding help in the field. David Philipp, Scott Smithers and Frank Phelan provided valuable information on the ecology of lakes in the Rideau and Gananoque River systems. The authors gratefully acknowledge the staff of the Queen's University Biological Station, and in particular, Frank Phelan for facilitating this work. Several anonymous referees kindly provided comments on an earlier version of the manuscript. The Ontario Ministry of Natural Resources kindly provided scientific collection permits for this research. Research activities were supported by an NSERC Discovery Grant to SJC and by an NSERC CGSD to MAG. All research was conducted with approval of the Canadian Council on Animal Care as administered through Carleton University and under scientific collection permits provided by the Ontario Ministry of Natural Resources.

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