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Parental care in response to natural variation in nest predation pressure in six sunfish (Centrarchidae: Teleostei) species

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Abstract – Parental care is an important, energetically costly component of the life history of many fishes. Despite this importance, little is known about how different species of fish vary parental care in response to natural nest predator burdens. In this study, underwater videography was used to quantify parental care activity of six species of syntopic nesting male centrarchid fishes in Lake Opinicon, Ontario, in response to natural predators. This approach was used to test the hypothesis that as offspring develop from eggs to wrigglers, parental care activity should decrease or remain static for fish guarding nests with low predator burden and increase for those with high predator burden, reflecting different external risks. Principal components analysis (PCA) was used to derive common aeration and nest defence variables. Aeration and predator defence activity of the fish varied extensively among species. Parental care behaviours indicative of defence and vigilance (e.g., turning, departures, time away from nest, displays) tended to be highest for species that had the most predation attempts, although this was not entirely consistent. There was also a positive relationship between the defence PCA metric and attempted predation. Defence did not vary with stage of offspring development, although interactions between defence and developmental stage were noted for several species. A trade-off between aeration and defence was not observed. In fact, species that provide high levels of aeration also simultaneously provide high levels of defence. Stage-specific patterns of defence in this study were less apparent than those documented by studies using responses to staged predator intrusions making it unclear as to the extent that fish were responding to the level of the risk to offspring than to the value of the brood. Therefore, combined use of observational and experimental assessments of parental care investment may be most appropriate for refining current theoretical paradigms.

S. J. Cooke[1,2], P. J. Weatherhead[2,3], D. H. Wahl[2,3], D. P. Philipp[2,3]

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON, Canada, [2]Center for Aquatic Ecology and Conservation, Illinois Natural History Survey, Champaign, IL, USA, [3]Program in Ecology, Evolution and Conservation Biology, University of Illinois, Champaign, IL, USA

Key words: aeration; parental care; predation; sunfish; videography

S. J. Cooke, Department of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, ON, Canada K1S 5B6; e-mail: steven_cooke@carleton.ca

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Introduction

Parental care is frequently studied to address questions related to ecological and evolutionary theory (e.g., Clutton-Brock 1991; Rosenblatt & Snowdon 1996) and to physiological energetics (e.g., Koteja 2000; Webb et al. 2002). There are numerous challenges to quantifying parental care activity in wild animals (Knight & Temple 1986) and these are particularly evident for aquatic organisms such as fish which can be difficult to observe. Most studies of parental care in fish have relied on staged predator intrusions, using either model predators (e.g., Colgan & Brown 1988; Ridgway 1988) or live predators constrained in clear containers (e.g., Urban 1991). Use of staged intrusions has the advantage of standardising the nature and

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timing of the threat to the nest and is effective for assessing whether different species conform to the same underlying patterns of care and investment. However, this approach overlooks potentially important variation in behaviour among individuals or species that might arise from natural variation in predation pressure on the developing offspring. For example, if natural predation pressure is higher on eggs than on fry, parents may have to invest more defending eggs even though staged intrusions indicate that parents value fry more than eggs. Knowledge of natural variation in parental behaviour is essential to understanding how factors such as nest predation pressure influence parental care and ultimately reproductive energetics. In this study, nonintrusive videography was used to quantify parental care activity relative to natural variation in nest predation risk in six syntopic species of centrarchid fishes, a group for which substantial background information on parental care is already available (Sargent 1997).

Parental investment theory predicts that parental care intensity will vary to reflect the changing needs of the offspring and their value (i.e., contribution of the current clutch to the parent's fitness) to the parent (Williams 1966; Trivers 1972). Because offspring become more valuable to the parent as they approach independence, parents should invest more and take greater risks protecting older offspring. However, because parental investment in current offspring is expected to reduce opportunities to invest in future offspring, parents should reduce care given to older offspring as the offspring become independent. A model developed by Sargent & Gross (1986) recognises that the dynamics of parental care reflect not solely the requirements of the offspring, but also the trade-offs between present and future reproduction. Thus, parental investment in fish should increase in intensity from the egg stage to the wriggler stage as offspring become more valuable, and then decrease as offspring become more independent. These predictions have been generally supported within centrarchids by studies using staged predator intrusions (Colgan & Brown 1988; Ridgway 1988; Ongarato & Snucins 1993). Parental behaviour of nesting birds assessed using staged intrusions also generally conforms to the patterns predicted from theory (Montgomerie & Weatherhead 1988).

Some attempts have been made to study natural variation in parental investment in fish using methods other than staged intrusions, although none have been able to explicitly and simultaneously evaluate the influence of natural nest predation burdens on parental behaviour. Colgan & Brown (1988) used snorkeling observations and stopwatches to observe parental care behaviour of four species of nesting sunfish. Although they relied on natural nest predator burdens and intrusion rates, it was not possible to obtain detailed information on different behaviours (e.g., egg fanning, nest defence) simultaneously. More recently, Cooke et al. (2002) used locomotory activity telemetry (i.e., measures swimming speeds) to evaluate the activity and energetics of bass (*Micropterus* spp.). This approach was effective for assessing the overall energy expenditure but provided little detailed information on specific behaviours. Interestingly, Cooke et al. (2002) found that patterns of parental investment based on locomotory activity for largemouth bass (*M. salmoides*) did not conform with theory or with experimentally derived patterns, indicating that natural patterns can deviate from those elicited experimentally.

Another alternative approach is to use underwater videography to document how natural predators affect parental care activity in fish. Hinch & Collins (1991) used this approach to monitor the behaviour of nesting smallmouth bass (*Micropterus dolomieu*), although in a lake with few predators, and Popiel et al. (1996) contrasted parental care of pumpkinseed (*Lepomis gibbosus*) in two lakes with different predator burdens. More recently, Steinhart et al. (2005) used videography to quantify smallmouth bass activity in response to a hyperabundant nest predator. In the current study, underwater videography was used to quantify parental care in six syntopic species of centrarchid fishes (smallmouth bass, largemouth bass, rock bass, *Ambloplites rupestris*, black crappie, *Pomoxis nigromaculatus*, pumpkinseed and bluegill, *L. macrochirus*).

In all species of centrarchids, the male constructs a nest, courts and spawns with one or more females, and then provides sole parental care for the offspring until they are independent. All males must also deal with common problems of aerating the eggs (Breder 1936). Against this common background, however, there are substantial differences among species (e.g., parental age, timing of reproduction, size of eggs, number of eggs, size of parent; for a summary of life-history variation among six species of centrarchids see Cooke et al. 2006) that should affect the risk of nest predation, and thus the need for nest defence. For example, the average parental male largemouth or smallmouth bass is approximately 230% longer and 700% heavier than the average parental male bluegill or pumpkinseed. Because all these fish nest in the littoral zone of the same bodies of water and thus confront the same array of potential nest predators, larger species should face lower risks of nest predation because they should have better capacity to defend the nest. Alternatively, because nests of larger species provide richer foraging opportunities to predators because of greater biomass of eggs or fry, larger species may experience as much or more risk of nest predation than smaller species, despite their size. During the parental care period, different species should invest differently in care because the contribution of the clutch to the parent's fitness varies with species' life-history (e.g., reproductive lifespan, number of clutches). Species such as bluegill which have multiple spawning bouts within a season, or longer-lived species such as largemouth bass and smallmouth bass should have higher expected future fitness relative to pumpkinseed, rock bass and black crappie (which are relatively short lived and typically spawn only once within a season).

Here, several specific predictions were evaluated. Within species, this study sought to determine whether predation risk or offspring age (nest stage) had a greater effect on nest defence. If predation risk to the offspring is relatively constant across nest stages, it was predicted that males should exhibit the same stage-specific variation in behaviour found in studies that use experimental intrusions to quantify parental care (i.e., care should increase as the offspring develop from eggs to wrigglers). If predation risk to the offspring varies among stages, however, there are two possible outcomes. Parental nest defence should increase from eggs to wrigglers if defence is determined primarily by brood value, whereas defence should be higher when risk of predation is higher if predator pressure determines defence. Among species, two predictions were tested. First, absolute activity devoted to nest defence should be greater for species whose offspring face higher predation risks. As argued above, predation risk could vary with the size of parents across species, so how variation in parental size affects interspecific variation in nest predation pressure was also investigated. Second, if parents make trade-offs between defending their nests and aerating eggs, then males of species that invest less in defence should be able to invest more in aeration. Aeration is important for both the egg and wriggler stages as it not only provides oxygen to developing offspring but also keeps the nest free of silt.

Materials and methods

Study site

This study was conducted from 1 May to 9 July 2001 in Lake Opinicon (44°33.30′N, 76°20.00′W), Ontario, the site of much previous research into the reproductive biology, parental care and early life history of centrarchid species [rock bass (Gross & Nowell 1980); pumpkinseed (Colgan & Gross 1977); black crappie (Colgan & Brown 1988); bluegill (Gross 1980); smallmouth bass (Cooke et al. 2002); and largemouth bass (Brown 1984; Colgan & Brown 1988; Cooke et al. 2002)]. All these species spawn throughout the littoral zone of Lake Opinicon (Keast et al. 1978). In this study, all these species can also serve as potential nest predators, but bluegill and pumpkinseed are by far the most abundant and frequent nest predators. Other possible nest predators include yellow perch, *Perca flavescens*, and brown bullhead, *Ameiurus nebulosus*. Relative to other lakes in the vicinity, Lake Opinicon has one of the highest burdens of potential nest predators (M.-A. Gravel, Carleton University, unpublished data). None of the potential nest predators in the lake are sufficiently large that they could consume any of the parental centrarchids engaged in care.

Data collection

Snorkeling surveys initiated when water temperature was 12 °C were used to locate nesting males. Small underwater cameras (AU-401; Atlantis, Bergenfield, New Jersey) and time-lapse recorders (SRT 7072; Sanyo, New York, New York) were used to record parental behaviour from multiple nests (Cooke & Bunt 2004). Although video is preferable to other techniques for quantifying parental care activity, there are some clear limitations. The biggest limitation is that it is only possible to observe the behaviour of the fish when it is within the camera's field of view. During the later stages of offspring development when fish may begin to patrol larger regions, or during absences when the fish leave the nest to engage predators, it is not possible to assess activity (Hinch & Collins 1991). The placement of the camera also has the potential to alter the behaviour of the parent as well as predators. Previous studies (e.g., Hinch & Collins 1991) used rather large cameras which required a cumbersome support stand. Innovations in camera design provided the opportunity to use a micro camera (roughly the size of a lemon) mounted on a narrow diameter (5 mm) aluminium rod that could be pushed between rocks or into soft substrate without mobilising sediment. Videography was chosen because it enabled the simultaneous monitoring of the parental care activity of nesting fish and predator activity less invasively than had snorkeling or SCUBA been used. Recording gear in a boat anchored at least 25 m from nests was connected to cameras by cables. Cameras were positioned 0.5 m from the nest by a diver and were on a 45° angle on a rod pointing down towards the nest. Ambient light provided illumination, so all video observations were obtained during daylight. Several studies of parental care in centrarchids have determined that activity rates remain unchanged at night (e.g., Hinch & Collins 1991; Cooke et al. 2002), so it was assumed that diurnal observations were also representative of nocturnal activity. Male parental behaviours were recorded between 10:00 and 14:00 h for a 10-min period during both the egg and wriggler stages. The egg stage is the period between egg deposition and hatching and the wriggler stage is the period from hatching to the fry swimming up (e.g., embryo in nest; Ridgway 1988). Video was only recorded from a given individual once so that it was unnecessary to control for 'individual' in analyses (e.g., Steinhart et al. 2005). At the conclusion of a video recording, the snorkeler recorded species and stage of offspring development, and estimated total length of the parental male to the nearest 2 cm (Table 1). In total, 210 individual nests were monitored yielding a sample size of between 12 and 20 nests per species at each stage of offspring development (Table 1), totalling 2100 min of video footage.

Video records were transcribed using a professional editing suite (Mitsubishi BV-100, Irvine, California) at playback speeds of 1/5 to 1/30 normal. Although 10 min of video was recorded, the first 5 min was excluded to eliminate any disturbance arising from camera placement. The same researcher conducted all transcription. Caudal and pectoral fin beat frequency of the fish while on the nest was quantified as this was indicative of fanning behaviours used to aerate the nest (Coleman & Fischer 1991). Defence metrics included turning rates, departures and display behaviours. Turning was assumed to indicate vigilance and hence defence (e.g., Hinch & Collins 1991) and was defined as a change greater than 45° in axial orientation over the nest. A nest departure was defined as the male leaving the view of the camera, which often involved the parental fish threatening or attacking nearby fish, but could also simply represent the fish departing for other reasons that were independent of predation (Hinch & Collins 1991; S.J. Cooke, personal observation). The methods used did not enable the differentiation of causes of nest departures. The percentage of the 5 min period the fish was absent was also recorded. Displays quantified were opercular flares and fin appression, both indicative of aggression (Poulsen & Chiszar 1975; Colgan et al. 1979). To assess nest predation burden, the rates of attempted and successful predation were recorded, the former involving a fish entering a male's nest and swimming towards the offspring or substrate, and the latter requiring that the predator make oral contact with the eggs or wrigglers. Nest departures were not included in estimates of predation pressure, and because some of these departures were likely responses to a predation attempt, it is possible that this study may have thus underestimated nest predator burdens.

Data analysis

Principal components analysis (PCA) of multiple variables was used to derive single variables for predator defence/vigilance (i.e., combining turning rates, departure rates, time away from nest and display rate) and aeration (i.e., combining pectoral and caudal fin rates). Raw data were log(10) transformed and PCA was conducted on the correlation matrix (Noy-Meir et al. 1975) using the latent root criterion to determine which components were significant (McGarigal et al. 2000). Two-way analysis of variance (ANOVA) was used to examine variation in parental care metrics among species at both developmental stages and within species for both stages. Tukey *post-hoc* tests were used to identify specific differences in parental care metrics when the ANOVA indicated significant results (Day & Quinn 1989). Spearman correlation analysis was used to test for relationships among pairs of parental care variables (including univariate and PCA-derived metrics as well as within-species for select variables) at both stages of offspring development for each of the six species. Bonferroni corrections were used to account for multiple comparisons (Day & Quinn 1989). All analyses were conducted using JMP-IN (V. 4.1; SAS Institute Inc., Carey, North Carolina) and all tests were considered significant at $\alpha = 0.05$ unless Bonferroni corrected.

Principal components analysis-derived variables were used for primary analyses and hypothesis testing. Univariate analyses were used to determine whether individual behaviours contributing to principal components varied similarly and to provide additional detail on parental care behaviour and activity. In studies of avian nest defence, individual behaviours

Table 1. Characteristics and sample sizes for videography data. The species are presented from smallest to largest (left to right) and are pumpkinseed (PS), bluegill (BG), black crappie (BC), rock bass (RB), smallmouth bass (SM) and largemouth bass (LB). Estimated total length (mm) values are summarised as mean and have SE bracketed below. The total number of predation attempts is provided for each species and stage of offspring development. The number of attempted predation events represents the total observed over a 10-min period summed for all fish of a given species at a given egg stage (i.e., for PS at the egg stage, 70 predation attempts were noted for $N = 20$ fish at 10 min per fish representing 200 min of video footage).

	Species					
Variable	PS	BG	BC	RB	SB	LB
Total Length (TL) of video fish (mm)	156.2 (1.6)	160.0 (1.9)	207.2 (3.7)	233.4 (4.6)	350.7 (5.9)	375.0 (6.4)
No. video fish – egg stage	20	20	20	19	17	17
No. total predation attempts noted – egg stage	70	51	0	72	6	60
No. video fish wriggler stage	18	19	12	14	17	17
No. total predation attempts noted – larval stage	57	15	2	56	5	0

are sometimes only weakly correlated with each other and with composite measures of defence, so tests of hypotheses can be sensitive to how one quantifies nest defence (Eckert & Weatherhead 1987; Gunness & Weatherhead 2002).

Results

Predation pressure

Predation attempts on offspring were generally positively correlated with rates of successful predation on offspring. During the egg stage this correlation was significant for most species (rock bass, $r = 0.76$; pumpkinseed, $r = 0.61$; bluegill, $r = 0.46$; largemouth bass, $r = 0.99$; black crappie, $r = 0.99$), but was significant for only one species during the wriggler stage (bluegill, $r = 0.89$). Attempted predation relative to species and stage of offspring development indicated that predation risk varied among species (Table 2, Fig. 1). The overall ANOVA model was significant, as was the main effect of species (Table 2). Neither stage of development nor the interaction between stage and species contributed significantly to the model (Table 2). Successful predation rates were low for all species and stages and did not vary significantly among species (Table 2, Fig. 1).

Nest defence

In the PCA of nest defence behaviours, PC1 accounted for 69% of total variation and had an eigenvalue of 1.81. All four behaviours loaded positively on PC1. Because PC2 explained only 16% additional variance, PC1 was used as the single measure of nest defence. Given that the risk of predation did not vary with the stage of offspring development, it was predicted that investment in nest defence should increase from egg to wriggler stage. There was a significant interaction between species and stage of development (Table 3, Fig. 2). Some of the smaller three species tended to exhibit a decrease in parental defence whereas the larger three species increased defence. However, none of these differences within species were significant, indicating overall consistency in defence activity during both the egg and wriggler stages (Fig. 2).

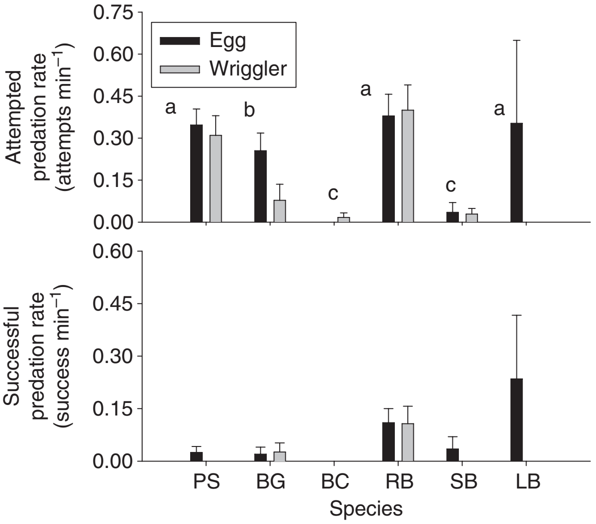

Fig. 1. Predation attempts and successful predation events on nests of six species of centrarchid fishes during the egg and wriggler stages of offspring development. Different letters indicate significant differences ($P < 0.05$) among species for the egg stage. There were no significant differences between stages within species. The species are presented from smallest to largest (left to right) and are pumpkinseed (PS), bluegill (BG), black crappie (BC), rock bass (RB), smallmouth bass (SM) and largemouth bass (LB). All values are mean + 1 SE.

Univariate analyses of the variables associated with nest defence and vigilance (i.e., turning rates, departure rates, time away from nest) yielded results that were generally consistent with the derived PCA assessment (Table 3, Fig. 3), suggesting that the composite PCA variable that was derived represents a robust approach for assessing defence. The exception was display rate, which was at times inconsistent with the PCA assessment. Display rate varied significantly by species and stage of offspring development, and also exhibited a significant interaction (Table 3, Fig. 3). Bluegill, smallmouth bass, and largemouth bass all significantly reduced their display rates between the egg and wriggler stages.

Aeration

In the PCA of aeration behaviours, PC1 accounted for 93% of total variation and had an eigenvalue of 1.85.

Table 2. anova model parameters for parental care activity metrics associated with predators for six sunfish during two stages of offspring development. For all parameters the main effect was species and the secondary effect was stage of offspring development.

Parameter	Source	*SS*	d.f.	*F*	*P*
Attempted predation rate	Species	3.89	5	4.57	<0.001
	Stage	0.40	1	2.36	0.126
	Species × stage	0.93	5	1.10	0.363
	Error	33.71	198		
Successful predation rate	Species	0.46	5	1.63	0.154
	Stage	0.12	1	2.19	0.141
	Species × stage	0.37	5	1.31	0.261
	Error	11.07	198		

Table 3. anova model parameters for parental care activity metrics associated with nest defence for six sunfish during two stages of offspring development. For all parameters the main effect was species and the secondary effect was stage of offspring development.

Parameter	Source	*SS*	d.f.	*F*	*P*
Defence PCA metric	Species	144.07	5	27.84	<0.001
	Stage	0.37	1	0.36	0.548
	Species × stage	26.30	5	5.08	<0.001
	Error	204.93	198		
Turning rate	Species	36438.83	5	121.35	<0.001
	Stage	19.96	1	0.33	0.565
	Species × stage	2966.94	5	9.88	<0.001
	Error	11890.61	198		
Departure rate	Species	5.93	5	4.09	0.002
	Stage	0.06	1	0.22	0.642
	Species × stage	5.38	5	3.70	0.003
	Error	57.49	198		
Time away	Species	222.63	5	6.73	<0.001
	Stage	0.12	1	0.02	0.892
	Species × stage	207.98	5	6.29	<0.001
	Error	1309.53	198		
Display rate	Species	8.06	5	15.11	<0.001
	Stage	0.45	1	4.21	0.041
	Species × stage	2.81	5	5.28	<0.001
	Error	21.12	198		

PCA, principal components analysis.

Both behaviours loaded positively on PC1. Because PC2 explained only 7% additional variance, PC1 was used as the single measure of aeration. It was predicted that if the risk of predation varied among species, investment in aeration should increase from the egg to the wriggler stage most for species with reduced predation risk (i.e., if fish are forced to trade-off investment in nest defence with investment in aeration, those that have to invest the least in defence have the greatest scope to vary aeration effort with changing offspring value). PC1 varied significantly among species, and with stage of development (Table 4, Fig. 2). However, there was a significant interaction between species and stage of development. Bluegill, the only species with colonial nests (and therefore some shared defence but also among-nest cannibalism) and frequent multiple broods within a season, decreased aeration during the wriggler stage, whereas largemouth bass increased aeration during the wriggler stage (Fig. 2). In general, it was the smaller species (i.e., those with higher risk of predation – excluding black crappie) that tended to exhibit heightened aeration activity (Fig. 2). Univariate analyses of the variables associated with aeration (i.e., caudal fin rate and pectoral fin rate) yielded results that were consistent with the derived PCA assessment (Table 4, Fig. 4).

Relationships among variables

Greater absolute investment for species facing higher predation risk was predicted. Using the PCA-derived defence metric, the relationship between defence activities and predation pressure was evaluated. A positive but nonsignificant relationship was observed for defence activities and attempted predation at both the egg ($r = 0.514$, $P = 0.296$) and wriggler stages ($r = 0.517$, $P = 0.293$). Conversely, no relationship was observed between defence and successful predation rates at either stage of offspring development (egg, $r = -0.236$, $P = 0.652$; wriggler, $r = -0.034$, $P = 0.949$).

To evaluate whether there was a trade-off between aeration and defence among species, correlation analyses on PCA-derived aeration and defence metrics was conducted. During the egg stage, there was a moderately positive, but not significant relationship between aeration and defence ($r = 0.590$, $P = 0.217$). During the wriggler stage there was a strong positive relationship between aeration and defence ($r = 0.897$, $P = 0.015$). The lack of a negative relationship suggests that there is not a trade-off between aeration and defence, and in fact species that provide more aeration also generally provide more defence and are able to engage in both activities simultaneously.

Within-species, positive correlations associated with general activity including caudal fin rate, pectoral fin rate, and turning rate were common, although these variables were not coupled for all species, or for all stages of offspring development (Table 5). It was assumed that turning rates were primarily associated with vigilance, and thus are a form of nest defence. However, the correlation between turning rate and measures of aeration suggests that turning may also be involved in aeration. Times away from the nest and departure rate were also highly correlated for several species (Table 5). Interestingly, there were also many instances where correlations were weak. For example, there were no significant correlations among defence variables apart from the time away from the

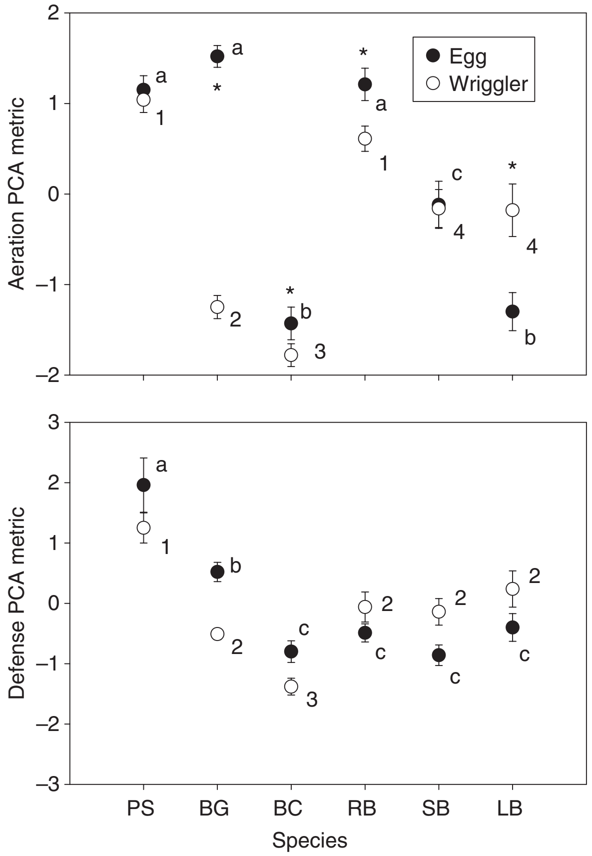

Fig. 2. Parental care metrics derived from principal components analysis for aeration and defence of six species of centrarchid fishes during the egg and wriggler stages of offspring development. Asterisks indicate significant differences ($P < 0.05$) among stages of development for individual species. Different letters indicate significant differences ($P < 0.05$) among species for the egg stage and different numbers indicate significant differences ($P < 0.05$) among species for the wriggler stage. The species are pumpkinseed (PS), bluegill (BG), black crappie (BC), rock bass (RB), smallmouth bass (SM) and largemouth bass (LB). All values are mean + 1 SE.

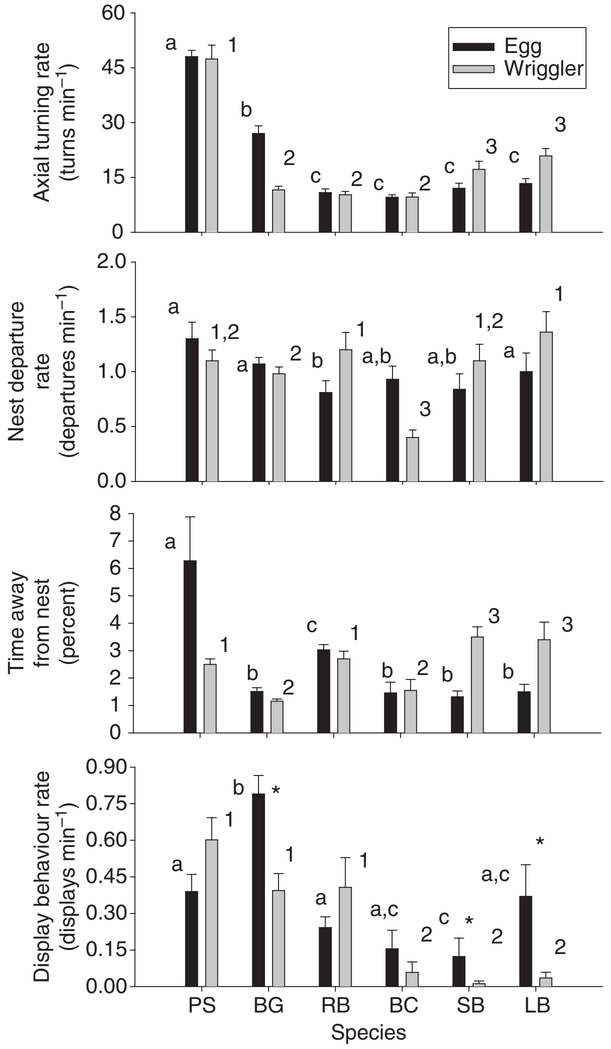

Fig. 3. Nest defence (turning rate, nest departure rate, time away from nest and displays) of six species of centrarchid fishes during the egg and wriggler stages of offspring development. Asterisks indicate significant differences ($P < 0.05$) among stages of development for individual species. Different letters indicate significant differences ($P < 0.05$) among species for the egg stage and different numbers indicate significant differences ($P < 0.05$) among species for the wriggler stage. The species are pumpkinseed (PS), bluegill (BG), black crappie (BC), rock bass (RB), smallmouth bass (SM) and largemouth bass (LB). All values are mean + 1 SE.

nest and departure rate. In general, there were few within-species correlations among variables that were examined.

Discussion

Underwater videography was used to quantify parental care dynamics of six syntopic centrarchid fishes to test the hypothesis that as offspring develop from eggs to wrigglers, parental care activity should decrease or remain static for fish guarding nests with low predator burden and increase for those with high predator burden, reflecting different external risks. Underwater videography has limitations in that the actual placement of the camera could influence the behaviour of the parental fish as well as potential nest predators, is limited in terms of the field of view, and a trade-off between the duration an individual nest is monitored and the ability to obtain observations from multiple individuals. Despite these limitations, the subtle camera placement techniques and the filtering of the first 5 min of video footage enabled the collection of more and better data from a large number of nesting fish than would have been possible through snorkeling or SCUBA techniques.

Within species it was predicted that brood defence should vary with offspring value (i.e., increase from egg stage to fry stage) only if predation pressure on eggs and fry was similar. Despite finding relatively uniform predation pressure across offspring stages,

Table 4. anova model parameters for parental care activity metrics associated with aeration and fanning for six sunfish during two stages of offspring development. For all parameters the main effect was species and the secondary effect was stage of offspring development.

Parameter	Source	*SS*	d.f.	*F*	*P*
Aeration PCA metric	Species	170.11	5	55.45	<0.001
	Stage	17.68	1	17.67	<0.001
	Species × stage	76.29	5	24.87	<0.001
	Error	121.48	198		
Caudal fin rate	Species	36508.81	5	60.76	<0.001
	Stage	955.07	1	7.94	0.005
	Species × stage	13101.35	5	21.80	<0.001
	Error	23794.07	198		
Pectoral fin rate	Species	26213.08	5	35.21	<0.001
	Stage	3310.50	1	22.23	<0.001
	Species × stage	14769.60	5	19.83	<0.001
	Error	29483.01	198		

PCA, principal components analysis.

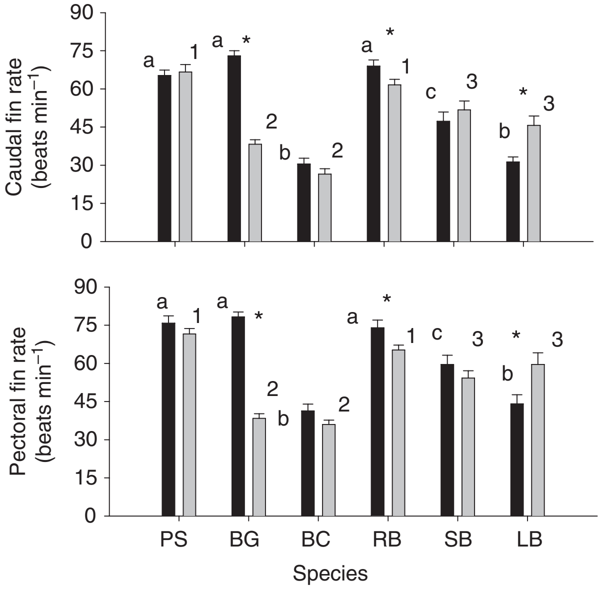

Fig. 4. Nest aeration (caudal fin rates and pectoral fin rates) of six species of centrarchid fishes during the egg and wriggler stages of offspring development. Asterisks indicate significant differences ($P < 0.05$) among stages of development for individual species. Different letters indicate significant differences ($P < 0.05$) among species for the egg stage and different numbers indicate significant differences ($P < 0.05$) among species for the wriggler stage. The species are pumpkinseed (PS), bluegill (BG), black crappie (BC), rock bass (RB), smallmouth bass (SM) and largemouth bass (LB). All values are mean + 1 SE.

there was no evidence that fry were defended more vigorously than eggs. This could mean that, unlike in staged trials with model predators, parental fish confronting real predators respond in a way that is largely independent of brood value. Interestingly, however, Urban (1991) reported that smallmouth bass also increased chasing behaviour in response to both greater brood predation pressure and increasing offspring age. Thus, brood value apparently still affected nest defence, but high predation pressure (relative to other systems; M.-A. Gravel, Carleton University, unpublished data) such as observed here may mask that effect in the current study. There is evidence from other taxa that parents confronted with natural predators respond differently when presented with model predators (e.g., Knight & Temple 1986), although there are also examples where responses have been similar (e.g., Kis et al. 2000). The best approach to resolving these contradictory outcomes will be to observe parental response to natural predators in a system in which predation pressure can be varied experimentally.

Predator burdens [both for the nest and the parent(s)] are increasingly being recognised as important variables in understanding parental care dynamics as more studies evaluate predation in natural systems with natural predators. Overall, little successful predation was observed during video observations, which was not surprising given the small temporal window that fish were monitored. Nonetheless, 384 predation attempts were recorded in the 2120 min of video observation (Table 1). Previous efforts to characterise predation rates on sunfish using video have been conducted in near predator-free environments (Hinch & Collins 1991) or with snorkeling (Colgan & Brown 1988; Urban 1991), or only on single species (Hinch & Collins 1991; Urban 1991; Popiel et al. 1996), and have suggested that predation rates are low, but risk can be high. An exception was a recent study by Steinhart et al. (2005) that examined predation pressure of an introduced hyperabundant nest predator on smallmouth bass nests. In this study, positive correlations were generally observed between the frequency of attempted and successful predation events for most species. Direct analysis of the relationship between the PCA defence metric and predation attempts yielded a moderately strong (but not significant) positive correlation across six species of sunfish. Previous research showed that sunfish engage almost all predators that attempt to prey on nests, irrespective of intruder species (Colgan & Brown 1988) and that high levels of defence behaviour by smallmouth bass is associated with high intrusion levels (Urban 1991).

Table 5. Significant correlations ($P < 0.05$, Bonferroni-corrected probabilities) for parental care metrics for six species of sunfish at two stages of offspring development. Correlation coefficients are for Spearman's rank correlations. Note that correlation analyses were attempted on all possible pairwise behavioural combinations and only those reported below were significant. Attempted predation and successful predation metrics were excluded from these analyses.

Pairwise	Offspring	Significant species correlation coefficients					
Correlations	Stage	PS	BG	BC	RB	SM	LM
Caudal fin rate – pectoral fin rate	Egg		0.81	0.85	0.49	0.87	0.97
	Wriggler			0.62		0.62	0.84
Caudal fin rate – turning rate	Egg						0.74
	Wriggler	0.63					
Pectoral rate – turning rate	Egg				0.69		0.79
	Wriggler					0.64	
Time away – departure rate	Egg	0.45		0.56	0.61	0.59	0.68
	Wriggler	0.60		0.88			0.87

PS, pumpkinseed; BG, bluegill; BC, black crappie; RB, rock bass; SM, smallmouth bass; LB, largemouth bass.

Absolute activity devoted to nest defence was predicted to be greater for species whose offspring face higher predation risks. Indeed, in this study, attempted predation rates were highly variable among species, with no apparent relationship with body size. Pumpkinseed (the smallest species) faced one of the highest levels of attempted predation and indeed they were the most active in terms of nest defence. The other species with high predation attempts, rock bass and largemouth bass, represent an intermediate and the largest species, respectively. Both of these species had relatively low responses in terms of defence. The risk of predation faced by individuals and species is varied and complex, reflecting factors such as water temperature (and its effect on the activity of predators), nesting habitat, nest size, food availability, predator density, breeding phenology, coloniality and detectability of the nest (Larsen et al. 1996). It was not possible to study all those factors here, which may contribute to some of the unexplained variance.

In terms of parental behaviour, it is possible that fish respond to other external factors apart from predation such as the number of offspring (Suski et al. 2003) or variable environmental conditions (Carlisle 1982; Cooke et al. 2003). However, recent analyses incorporating multiple variables in birds have revealed that predation pressure was the primary factor in shaping parental care (Larsen et al. 1996). Similarly, Cooke et al. (2003) determined that smallmouth bass that experienced variable environmental conditions did not vary parental care investment in a predictable or consistent manner. Instead, because nest predators were scarce and nest density was high in that study, the authors concluded that the nest predator burden might strongly influence the level of parental investment. Urban (1991) also determined that a high intruder level was an important factor for smallmouth bass resource allocation to parental care, but that nest predator burden did not influence nest desertion. Clearly, there is a need for additional research into various taxa that involves systematically varying predator densities and risk factors to identify the extent to which nest defence levels across species is influenced by nest predation risk.

It was predicted that there would be a trade-off between defence and aeration that would reflect short-term variation in predation pressure enabling fish with low predator risk (and hence low defence activity) to invest more in aeration (e.g., Jones & Reynolds 1999). Indeed, previous research supports the notion that antipredator behaviour has a cost to other parental care behaviours (such as aeration; Magnhagen 1991). Interestingly, no trade-off between aeration and defence was observed. Instead, it was determined that fish providing high levels of defence also provided high levels of aeration. The expectation of a trade-off between defence and aeration was based on the assumption that aeration behaviour serves no defensive purpose. Given that turning rate was highly correlated with aeration, however, defence and aeration may not be as clearly differentiated as had been assumed in this study. If the first reaction of a nest-guarding fish to a potential predator is to increase its general level of activity just to signal its presence, this could result in both 'aeration' and nest defence increasing in response to higher risk of predation. If this hypothesis is correct, one would expect that those species exhibiting high rates of aeration in this study should reduce aeration (with no deleterious effects on offspring) if predation threats were experimentally reduced.

The results of this study suggest that researchers studying parental care in fish and other taxa should attempt to quantify natural predator intrusion rates and natural predators, besides using manipulations of the density of natural predators. Because parental care involves trade-offs of current and future reproduction, a useful goal is to quantify those trade-offs, using energy as a currency (Calow 1985; Webb et al. 2002). These approaches are particularly appropriate for estimating how much energy parents expend, and the implications of that expenditure for their survival and future reproduction. Whereas staged intrusions are useful for determining how parents value offspring, only parental care expenditures relative to natural predator burdens tell us how much parental care actually costs.

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