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Energetics of parental care in six syntopic centrarchid fishes

Received: 25 July 2005 / Accepted: 19 January 2006 / Published online: 17 February 2006
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Abstract We studied parental behavior in six syntopically breeding species of centrarchid fishes to determine whether energetic costs could contribute to our understanding of the diversity of parental care. We used a combination of underwater videography, radio telemetry and direct observation to examine how the cost of parental care varied with both its duration and intensity. Duration of parental care, activity patterns, and energetic costs varied widely among species. Overall, the duration of care increased with parental size between species. When energetic costs were adjusted for species-specific differences in the duration of parental care, the cost of parental care also increased with mean size of the species. Species with extended parental care exhibited stage-specific patterns of activity and energy expenditure consistent with parental investment theory, whereas fish with short duration parental care tended to maintain high levels of activity throughout the entire period of parental care. The only apparent exception (a species

with brief parental care but stage-specific behavior) was a species with multiple breeding bouts, and thus effectively having protracted parental care. These data suggest that some species with short duration parental care can afford not to adjust parental investment over stages of offspring development. Using our empirical data on parental care duration and costs, we reevaluated the relationship between egg size and quality of parental care. Variation in egg size explained almost all of the observed variation in total energetic cost of parental care, and to a lesser degree, duration—the larger the eggs, the more costly the parental care. This research highlights the value of incorporating energetic information into the study of parental care behavior and testing of ecological theory.

Keywords Activity patterns · Centrarchid fish · Egg size · Energetic costs · Parental care

Communicated by Carol Vleck

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Introduction

Parental care is an energetically costly activity, the duration and intensity of which vary widely, both within and among species (Baylis 1978; Clutton-Brock 1991). In addition to energetic costs, there can also be significant time expenditures (Clutton-Brock and Parker 1992). Past research efforts have focused primarily on determining how ecological factors influence parental care and on defining the relationship between parental care and mating systems (see Clutton-Brock 1991; Rosenblatt and Snowdon 1996). Consistent with the growing integration of the fields of ecological physiology and behavioral ecology (Feder et al. 1987; Altmann and Altmann 2003), there has been growing interest in understanding the energetic consequences of parental care (e.g., Masman et al. 1989; Balshine-Earn 1995; Webb et al. 2002). Indeed, the currency that controls or otherwise limits parental investment for either current or future reproductive effort is the energetic and physiological condition of the parent (Calow 1979; Webb et al.

2002). If the parent lacks the energetic resources either to reproduce or to provide adequate parental care, their lifetime fitness will suffer accordingly. Despite the apparent importance of energetics in parental care decisions (Webb et al. 2002), the difficulty in quantifying energy expenditure by organisms in their natural environments (e.g., Butler 1989; Cooke et al. 2004) has made studying the energetics of parental care challenging (Cooke et al. 2002). Few studies to date have combined reliable measures of the duration of parental care with information on the intensity of parental care activities to determine the total energetic cost of parental care. Here, we undertake such a study to explore how body size, duration of parental care and size of eggs explain variation in energy expenditure that exists among six species of centrarchid fishes.

Perhaps the best information on the energetics of parental care in fish can be found for the centrarchid family of teleost fishes. Parental care arose in proto-centrarchids and is a characteristic that helps to define the family Centrarchidae (Gross 1980). 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 (Breder 1936). Within this general framework, however, there is considerable inter-specific variation. To date, most studies of parental care energetics, including those on centrarchids, have focused on only a single species (e.g., Coleman and Fischer 1991; Hinch and Collins 1991; Sabat 1994; Mackereth et al. 1999; Gillooly and Baylis 1999) or only two species (e.g., Cooke et al. 2002; see Garland and Adolph 1994). Collectively, these studies point towards the importance of energetics in determining the ability of the animals to provide adequate care. However, because these studies have been conducted on different species, in different environments, in different seasons, and using different techniques, direct comparisons between them are difficult. Therefore, we studied the paternal care energetics of six species of centrarchid species that occur syntopically in Lake Opinicon, Ontario: smallmouth bass, *Micropterus dolomieu*; largemouth bass, *M. salmoides*; rock bass, *Ambloplites rupestris*; black crappie, *Pomoxis nigromaculatus*; pumpkinseed, *Lepomis gibbosus*; and bluegill, *L. macrochirus*. In addition to the aforementioned reasons for choosing these species, there is also a substantial literature on the life history of these species that we draw upon to aid in interpreting our findings.

Body size profoundly affects the energetics and physiological ecology of fishes (Schmidt-Nielsen 1984). Allometric functions result in negative relationships between body size and mass specific metabolic rate (Brett and Groves 1979; Gillooly et al. 2001) and between body size and the cost of locomotion (Schmidt-Nielsen 1972). There is a positive relationship, however, between body size and energy reserves (Calow 1985). Size-based variation in available energy has been shown to affect energy reserves, and hence the ability to provide extended care for smallmouth bass (Mackereth 1995;

Mackereth et al. 1999; Gillooly and Baylis 1999; Cooke et al. 2002) and largemouth bass (Cooke et al. 2002). Sabat (1994) also noted that male rock bass that lost the most mass during parental care were the individuals least likely to be observed in subsequent years, indicating a negative effect of current parental investment on future reproduction. For centrarchid fishes, adult males must acquire sufficient resources to accumulate the lipid reserves required to survive the winter (Sullivan 1985). For parental male fish, growth is thus typically limited to the summer and fall, after reproduction. Somatic growth and reproduction only occur when resources are acquired in excess of that threshold (Calow 1985). The magnitude of size variation observed among species of centrarchid fish is much greater than that observed within species, suggesting that absolute size may constrain aspects of parental care behavior in certain species (Wiegmann and Baylis 1995). Our first objective was to evaluate the importance of body size in determining the patterns of investment in parental care. Given the documented effect of variation in size within a species on parental care, we predicted that the energetic constraints of body size on parental care would be more extreme among species. Specifically, when standardized to a common mass, parental care should be more costly for smaller species than for larger species. For this reason, smaller fish should be under a greater constraint to budget energy expenditure efficiently during parental care.

Some species of centrarchid fishes defend their broods more aggressively than others (e.g., Colgan and Brown 1988), and some species stay with their young much longer than others (Breder 1936). Regardless of duration, this parental care is energetically costly (Hinch and Collins 1991; Cooke et al. 2002). Furthermore, energy intake by parental fish is usually reduced because foraging opportunities are limited (Hinch and Collins 1991; Mackereth et al. 1999). Our second objective was to determine how the intensity of parental care varies as offspring develop from the egg to wriggler (free embryo) stage for fish with different durations of parental care. Theory predicts that parents vary parental care intensity to reflect both the changing needs of the offspring and the changing value of those offspring to the parent, as a result of the trade-off between budgeting for current versus future reproduction (Trivers 1972; Sargent and Gross 1986; Montgomerie and Weatherhead 1988). Parental investment should increase from the egg stage to the hatched embryo stage as the offspring develop, and then fall as offspring approach independence. These predictions have been generally supported by empirical studies (Colgan and Brown 1988; Ridgway 1988; Ongarato and Snucins 1993), although some deviations have been noted (e.g., largemouth bass, in Cooke et al. 2002). If energy is the principal constraint on parental care (as opposed to risk of predation, for example), we predict that in species that have relatively brief periods of parental care, parental males should be able to sustain high levels of care throughout the parental care period.

Thus, they should exhibit relatively low variation in parental care between egg and wriggler stages. Conversely, in species with extended parental care, there should be more pressure on parents to budget their available energy. Thus, investment should vary more across the various developmental stages of the offspring, and activity levels should be lower overall, than for species with short periods of parental care. We also predict that bluegill would be an exception to this general pattern, because despite exhibiting brief parental care per spawning bout, they spawn repeatedly within years (Breder 1936; Coleman and Fischer 1991). Thus, assuming parental bluegills cannot replace depleted energy reserves between spawning bouts, functionally they should be similar to species with more extended parental care.

Among organisms that provide parental care, the quality of care generally increases with the size of the eggs (Sargent et al. 1987). Several competing models have attempted to explain this correlation: (1) parental care favored the evolution of larger eggs (Shine 1978; Sargent et al. 1987); (2) larger eggs favored the evolution of parental care (Nussbaum 1985); (3) parental care and large egg size co-evolved (Nussbaum and Schultz 1989); or (4) some additional selective pressure simultaneously favored parental care and large egg size (Shine 1989). It remains unclear which of these alternatives is correct. This lack of resolution may be related to two potential problems with how parental care has been quantified. First, some researchers have equated the quality of parental care with the duration of care (e.g., Shine 1978). As we have argued above, the cost (and presumably the quality) of parental care should vary not only with the duration of the parental care, but also with its intensity. Second, the duration of parental care may not have been quantified correctly in previous studies of centrarchids. Parental care has typically been assumed to end when the parental male fish and its offspring are no longer at the nest site. In some centrarchids, however, care extends well beyond the nest-guarding phase (e.g., small-mouth bass and largemouth bass; Cooke et al. 2002). The mobility of both the adult male and his offspring makes determining the true duration of parental care difficult. If the duration of parental care has been estimated inaccurately for some species, then the relationship between parental care quality and egg size may differ from the pattern identified by Sargent et al. (1987). Therefore, our third objective was to re-evaluate the relationship between egg size and parental care quality. Because larger eggs take longer to develop (Steele 1977), and thus require more extended parental care than smaller eggs, we still expect a positive correlation between the duration of parental care and egg size. By examining the components of parental care (duration, intensity, total energetic cost) separately, we will refine our understanding of the relationship between egg size and parental care.

It was critical to our objectives that we accurately quantified both the intensity and duration of parental

care in the six species we studied. Detailed accounts of parental care intensity for centrarchids are generally lacking due to the difficulty in simultaneously quantifying and recording different behaviors while snorkeling. Also, as mentioned above, documenting the duration of parental care has been ambiguous because parental care may continue after the fish leave the nest. To overcome these difficulties we employed a multi-faceted approach to observe the fish. To evaluate parental care intensity (i.e., vigilance, turning rates, fanning rates), we used underwater videography in combination with snorkeling observations. To document the duration of parental care, we used small radio transmitters coupled with snorkeling to locate parental fish, particularly following nest departure. We estimated the energetic cost of parental care by combining our data on parental care intensity with published values on metabolic rates associated with various behaviors. Although there are some limitations to using published values, this is a widely accepted means of exploring bioenergetic hypotheses in fishes (Ney 1993). We then used our data on the duration of parental care to estimate the total costs of parental care for different species.

Materials and methods

Subjects and study site

We considered parental care to include the period from fertilization until the parent deserts the offspring. We recognize that parental investment can include nest construction, courting, and the actual spawning event, all of which can be costly (Cooke et al. 2001). However, it was not possible to quantify these variables in this study. This study was conducted in Lake Opinicon (44°33'30"N, 76°20'00"W), Ontario, from 1 May to 9 July 2001. In addition, we supplemented the radio telemetry study of black crappie by monitoring six additional fish from 16 May to 7 June 2002 during a period when water temperatures were the same as in 2001. Lake Opinicon has served as the focus for a great deal of previous research on the reproductive biology, including parental care and early life-history, of centrarchid species (e.g., rock bass, Gross and Nowell 1980; pumpkinseed, Colgan and Gross 1977; black crappie, Colgan and Brown 1988; bluegill, Gross 1980; small-mouth bass, Philipp et al. 1997; Cooke et al. 2002; and largemouth bass, Brown 1984; Colgan and Brown 1988; Cooke et al. 2002). The life-history traits of these species are well documented and have been the subject of an entire book (Carlander 1977). However, one common pattern is the fact that there is extreme variation in life-history traits among populations of the same species (and across latitudes). Consequently, it is not possible to present a brief summary of the life-history characteristics for all six species. However, we will identify key aspects of different species life-history strategies as required to aid in our interpretation of findings. All six of

these species occur naturally in Lake Opinicon and spawn in the littoral zone throughout the lake (Keast et al. 1978). To facilitate frequent monitoring of nests and to avoid heavy angling pressure, we used a study site close to the Queen's University Biological Station that included ~4 km of shoreline. All experiments were approved by the University of Illinois Office of Laboratory Animal Research and the Queen's University Animal Care Committee. All procedures were in accordance with the guidelines for animal research in Canada and the United States. Scientific Collection Permits were furnished by the Ontario Ministry of Natural Resources.

Snorkeling and telemetry

Snorkeling surveys, initiated when the water temperature reached 12°C, were used to monitor the onset and progression of reproduction by all six centrarchid species. Snorkelers swam the study site every 2–3 days. When nests were found, numbered tiles were placed adjacent to nests, the male was identified to species and his total length estimated to the nearest cm by trained divers, and the offspring stage was recorded. We used externally attached radio transmitters for monitoring the parental care duration of nest guarding fish because this method is rapid, less invasive than internal implantation, and does not require anesthetizing the fish. Furthermore, a recent study by Cooke (2003) determined that the same transmitters and methods we used here did not result in any changes in behavior or reproductive success relative to control fish for rock bass. These methods were developed with veterinarian consultation and used our extensive experience in transmitter attachment on fish and other animals. For this study, all transmitter attachments were conducted on a research vessel equipped with a surgical table. We located nesting males that were attending eggs or newly-hatched larvae and then angled these parental males from their nests using rod and reel. Fish were landed within 10 s and immediately placed ventral side down on a wet sponge pad where they were measured and weighed (Table 1). A wet cloth covered the head and caudal peduncle region of the fish while an assistant held the fish in place for transmitter attachment. A neoprene backing plate was placed on two 22-gauge hypodermic needles mounted on 3-ml syringes that were pushed through the dorsal back musculature, ventral to the junction of the soft and spiny dorsal fins (Beaumont et al. 1996; Cooke 2003). From the opposite side, the transmitter attachment wires (surgical stainless steel, 20 gauge) that had already been threaded through the transmitter (Model BD-2G, Holohil Systems, Ontario; wgt in air, 2.1 g, 14×6×4 mm, 120 mm antenna wire for small fish and Model AVM G3, AVM Instruments, Calif., wgt in air, 3.6 g, 18×9×6 mm, 200 mm antenna wire for large fish) and a neoprene pad (2 mm) were inserted into the lumen of the needles. The wires were pulled out on the opposite side of the fish, and when the needles were removed, the

neoprene backing plate was left in place to protect the body of the fish. The wires were twisted carefully and trimmed prior to releasing the fish above its nest. The fish were out of water for less than 90 s. A snorkeler protected and monitored the nest during the attachment procedure until the fish had resumed parental care duties. At the time of this study, we used the smallest commercially available radio transmitters. Nonetheless, we were forced to select larger individuals (especially for the smallest species) relative to the broader population of nesting fish. Consequently, the size of fish monitored with telemetry were larger than those monitored with videography (see below).

During the early stages of offspring development, the presence/absence of the nest-guarding males equipped with transmitters was determined by a snorkeler. As fish approached the period at which they would normally terminate care or move from the nest with their offspring, we located each fish using telemetry. We used programmable radio telemetry receivers equipped with two-element H antennas. Initially, we used a combination of triangulation and pinpointing fish through gain reductions to locate the radio-tagged fish. When we were within 10 m of a radio-tagged fish, we dispatched one or more snorkelers to search visually for the fish. Simultaneously, we switched to an electric trolling motor to maneuver the boat. We continued reducing gain until we had a strong signal with a gain of "0". Marker buoys were deployed and the boat was moved from the immediate area. Upon visually locating the fish, the diver recorded information on the general condition of the male, the activity and behavior of the male, and determined the presence or absence of offspring. When a fish was located on two successive occasions without offspring or engaged in activity unrelated to parental care, we assumed that care had terminated on the last day that parental care was observed. During these snorkeling observations we observed no ill effects of the transmitters on the tagged males.

Videography

We used small underwater cameras (Atlantis, AU-401) and time-lapse recorders (Sanyo, SRT 7072) to record detailed information on multiple nests. Our videographic observations were restricted to fish that were not carrying transmitters. Video recording gear was located aboard a boat that was anchored at least 25 m from the nest sites. Each camera had a 50-m cable that connected it to the boat. Cameras were positioned 0.5 m from the nest by a diver and were on a 45° angle pointing down towards the nest (Cooke and Bunt 2004). Because we relied on ambient light to provide illumination for the camera, all of our video observations were diurnal. Several studies of parental care in centrarchids have determined that activity rates remain unchanged at night (e.g., Hinch and Collins 1991; Cooke et al. 2002), so we assumed that our diurnal observations were also

Table 1 Summary of data collected using telemetry, snorkeling, and videography for six species of centrarchid fishes and basic life-history information

Variable	Species					
	RB	PS	BG	SB	LB	BC
TL of transmitter fish (mm)	255.3 (4.8)	190.5 (3.8)	194.3 (2.0)	364.5 (10.9)	352.8 (6.9)	231.6 (6.6)
Mass of transmitter fish (g)	309.9 (14.6)	140.7 (7.3)	129.9 (5.3)	691.5 (11.5)	597.4 (18.6)	169.2 (6.9)
Number of transmitter fish	13	12	12	13	14	12
Duration of care (days)	14.5 ^a (1.2)	6.0 ^{b,c} (0.4)	4.3 ^b (0.1)	28.4 ^d (2.2)	20.3 ^c (1.0)	10.7 ^{a,c} (0.5)
TL of video fish (mm)	233.4 (4.6)	156.2 (1.6)	160.0 (1.9)	350.7 (5.9)	375.0 (6.4)	207.2 (3.7)
Mass of video fish (g)	251.4 (13.0)	82.1 (2.1)	75.2 (2.5)	638.5 (42.9)	794.9 (45.9)	118.1 (5.8)
Number of video fish egg stage	19	20	20	17	17	20
Number of video fish wriggler stage	14	18	19	17	17	12
Water temperature during care (°C)	19.6 ^{a,b} (0.2)	21.3 ^c (0.3)	23.8 ^d (0.4)	19.8 ^b (0.3)	20.3 ^b (0.3)	18.0 ^a (0.3)
Egg diameter (mm)	3.07 ^a (0.04)	1.50 ^b (0.02)	1.47 ^b (0.02)	3.11 ^a (0.03)	2.09 ^c (0.03)	1.27 ^d (0.02)
Egg mass (g)	0.00531 ^a (0.00009)	0.00063 ^b (0.00002)	0.00083 ^b (0.00001)	0.00717 ^a (0.00010)	0.00212 ^c (0.00003)	0.00044 ^d (0.00001)
Fecundity	3,000–1,100	1,700–2,900	7,000–38,000	2,000–21,000	17,000–21,000	37,000
Age at maturity (years)	3–6	2–3	1–3	3–4	3–4	2–4
Longevity (years)	10–12	8–10	7–10	8–16	10–18	8–10
Size of larvae at hatch (mm)	NA	2.6–3.1	2–3	4.6	3.6–4.1	2.3

Dissimilar letters indicated significantly different values among species (Tukey–HSD: $P < 0.05$) following one-way ANOVA for duration of care, water temperature, and egg sizes. For egg size analyses, $n = 15$ nests per species. All mean values have SE bracketed below. Life-history data for fecundity, age at maturity, longevity, and size of larvae at hatch were obtained from the literature. Primary sources were Froese and Pauly (2005; i.e., Fishbase; <http://www.fishbase.org>), Carlander (1977), and Scott and Crossman (1973). We attempted to obtain data from populations in Canada or at the northern part of the centrarchid range. Note that these values are intended to highlight general patterns as there is substantial intraspecific variation. Also note that fecundity refers to the number of eggs per female and does not necessarily translate into the number of eggs deposited in a single nest. Some species such as bluegill typically spawn with multiple females whereas others such as smallmouth bass rarely spawn with multiple females

RB rock bass; PS pumpkinseed; BG bluegill; SB smallmouth bass; LB largemouth bass; BC black crappie; NA not available

representative of nocturnal activity. We recorded male parental behaviors for fish not equipped with radio transmitters between 1000 and 1400 hours for a 10-min period during both the egg and wriggler stages. The egg stage is the period after egg deposition and fertilization, but prior to hatching. The wriggler stage occurs after eggs had hatched, but prior to them becoming free swimming. We only recorded video footage from each individual once so that we did not have to control for individuals in analyses. At the conclusion of the video recordings, the snorkeler recorded the species, the size of the fish, and examined the stage of offspring development (Table 1).

We transcribed video records using a professional editing suite (Mitsubishi BV-100) at playback speeds of 1/5 to 1/30 normal. Although we recorded at least 10 min of video, we excluded the first 5 min to eliminate any disturbances arising from camera placement. We quantified the caudal fin beat frequency of the fish while on the nest and used those values to calculate the in-place swimming speed of the male. We used methods outlined in Hinch and Collins (1991) to establish

swimming speeds and to ascribe energetic costs to swimming speeds (Weihs 1977). We quantified swimming speed using videography because it can be used to quantify activity costs when incorporated into existing energetics models (Boisclair and Legett 1989; Trudel and Boisclair 1996) and because it has been determined to be a robust behavioral indicator of fish energetics (e.g., Trudel and Boisclair 1996; Rennie et al. 2005). We used the Wisconsin Bioenergetics model (Hanson et al. 1997), a widely used tool in fisheries science (Ney 1993) that has benefited from substantial ground truthing and refinement. To derive energetic costs from behavioral data, we replaced the activity multiplier of the Wisconsin Bioenergetics model with our empirically determined data. We also had to modify model parameters using species-specific criteria derived from the literature because the Wisconsin model had not been parameterized for all six species. Also, even where existing models were available, we modified them to incorporate the most thermally relevant swimming energetics information. For example, we used previously developed information on metabolic costs of swimming for largemouth bass

Table 2 Summary of bioenergetics information used for establishing the energetic costs of parental care for six species of centrarchid fishes

Species	Bioenergetic model information	Temperature (°C)	Parameter modifications
RB	Respiration Equation 2, smallmouth bass adult model developed by Shuter and Post (1990)	18	Used swimming/respiration costs for smallmouth bass (see SB, below)
PS	Respiration Equation 2, bluegill adult model developed by Kitchell et al. (1974)	22	Incorporated swimming/respiration costs from Brett and Sutherland (1965) and Evans (1984)
BG	Respiration Equation 2, bluegill adult model developed by Kitchell et al. (1974)	24	Incorporated swimming/respiration costs from Wohlschlag and Juliano (1959)
SB	Respiration Equation 2, smallmouth bass adult model developed by Shuter and Post (1990)	18	Incorporated swimming/respiration costs from Cooke (unpublished data)
LB	Respiration Equation 1, largemouth bass adult model developed by Rice et al. (1983)	20	Incorporated swimming/respiration costs from Beamish (1970)
BC	Respiration Equation 2, bluegill adult model developed by Kitchell et al. (1974)	16	Incorporated swimming/respiration costs from Parsons and Sylvester (1992)

Data provided include which type of bioenergetics model was used and the authors (corresponds to Wisconsin Bioenergetics Model; see Hanson et al. 1997), the water temperature used for modeling, and data sources for parameter modifications associated with the respiration component of the models
RB rock bass; *PS* pumpkinseed; *BG* bluegill; *SB* smallmouth bass; *LB* largemouth bass; *BC* black crappie

(Beamish 1970), pumpkinseed (Brett and Sutherland 1965; Evans 1984), and bluegill (Wohlschlag and Juliano 1959). Data for smallmouth bass were derived from data collected at 18°C (S.J. Cooke, Unpublished data). Because no empirical data were available for rock bass and because smallmouth bass and rock bass have similar thermal preferences and tolerances (Wismer and Christie 1987), as well as Q_{10} rates (S.J. Cooke, Unpublished data), we used smallmouth bass model parameters for rock bass calculations. Data were also unavailable for black crappie, so we used values collected for white crappie (Parsons and Sylvester 1992) because these fish have very similar life histories and physiological characteristics (Scott and Crossman 1973; Wismer and Christie 1987). Use of metabolic values from similar species when data are unavailable is a recognized technique in fish bioenergetics (Ney 1993). Our specific modifications to the models are listed in Table 2. Because metabolic rates vary with water temperature (Beamish 1964; Brett and Groves 1979), and because water temperatures during parental care differ among species, we used water temperatures measured in Lake Opinicon during each species' parental care period for estimating their respective parental care activity costs (see Tables 1, 2, Fig. 1). Oxycaloric equivalents were calculated for oxygen consumption values and then expressed in joules (Brett and Groves 1979). Because these data are redundant with oxygen consumption data, we use them only for descriptive purposes. We adjusted all values for the size of the fish using the generalized mass scaling exponent of 0.8 where required (Schmidt-Nielsen 1984). Where appropriate we standardized values to 1 kg for comparative purposes.

Egg measurements

We collected newly fertilized eggs from 15 nests of each study species. Eggs were held in lake water for no more than 2 h, dried with a paper towel and weighed in groups of ten (one group per nest) using a Metler AE 100 scale (0.0001 g). We then used a dissecting microscope at 160× magnification equipped with an ocular micrometer to measure the diameter of ten eggs from each nest.

Phylogenetic corrections

Phylogenetic relatedness poses a potential constraint for comparative studies because closely related species can share a certain character state through common ancestry rather than through independent evolution (Felsenstein 1985; Harvey and Pagel 1991). As a result, we conducted our analysis with and without controlling for phylogenetic effects. To control for phylogenetic effects, data were converted to phylogenetically independent standardized contrasts using the PDTREE module of the Phylogenetic Diversity Analysis Package (PDAP, v.6.0)

(Garland et al. 1992; 1993), which is based on the methods of Felsenstein (1985). Branch lengths were transformed prior to analyses using Grafen's (1989) method for arbitrary branch lengths. We used a phylogeny obtained from a molecular genetic analysis by Roe et al. (2002), which included all the species we examined except for pumpkinseed. Because morphological (Mabee 1993) and genetic evidence (Neff et al. 1999) suggest that pumpkinseed are closely related to bluegill, the other *Lepomis* species, we considered pumpkinseed to be a separate branch, originating at the *Lepomis* node. The branch length for pumpkinseed was arbitrarily assumed to be the same as bluegill. Branch lengths provided for several other *Lepomis* in Roe et al. (2002) were all of similar length. To provide phylogenetic consistency throughout the manuscript, species are listed in order of evolutionary history in all tables and figures.

Data analysis

One-way analysis of variance with the conservative Tukey HSD test (Day and Quinn 1989) was used to assess differences in fish size, egg size, and duration of parental care among the species we examined. Pairwise correlations were also used to test for relationships in duration of parental care and size of fish among species. *T*-tests were used to compare parental care activity and energetic parameters among stages of offspring development for each species. One-way ANOVA was also used to compare total respiration rates and energetic costs for each species corrected for duration of care. We used multiple stepwise regression analysis to determine which parental care factors explained significant variation in

egg diameter and mass. We used phylogenetically independent contrasts (PICs; see above) to account for phylogenetic influences and have reported these data in addition to phylogenetically uncorrected data throughout the results. All analyses were conducted using JMP-IN (v.4.1, SAS Institute) and all tests were considered significant at $\alpha=0.05$.

Results

Relationships between parental care and parental body size

Duration of parental care varied significantly among the six species (ANOVA: $F_{5,75}=59.2$, $P<0.001$), ranging from a low of 4.3 days (at 23.8°C) for bluegill to a high of 28.4 days (at 19.8°C) for smallmouth bass (Table 1). Consistent with our prediction, duration of parental care among species increased significantly with average size of parental males for each species ($r_s=0.966$, $P=0.002$; $rs_{PIC}=0.969$, $P=0.006$). Water temperatures during parental care varied among species (ANOVA: $F_{5,182}=23.7$, $P<0.001$), with black crappie experiencing the lowest temperatures and bluegill the highest temperatures, consistent with the seasonal progression of reproduction (Table 1; Fig. 1). However, duration of care among species was not correlated with mean water temperature during the parental care period.

Relative swimming speeds were consistently higher for smaller fish as evidenced by negative correlations between body size and swimming speeds (Table 3). Absolute respiration rates differed among species for both egg (ANOVA: $F_{5,107}=75.1$, $P<0.001$) and wriggler

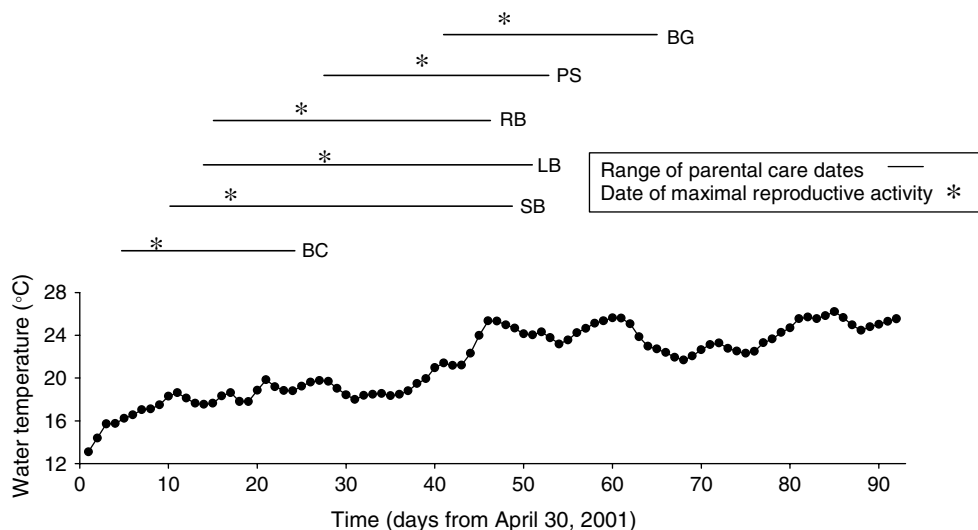


Fig. 1 Reproductive activities of male centrarchid fishes in Lake Opinicon during 2001. The date of first spawn and termination of care are denoted on the figure by lines for each species (BG bluegill; PS pumpkinseed; RB rock bass; LB largemouth bass; SB smallmouth bass; BC black crappie). Mean daily water temperature

(1.2 m depth) was plotted for a 3-month period that encompassed all centrarchid reproduction. Asterisks (*) indicate the date of maximal reproductive activity (i.e., the most active nests within the study site)

Table 3 Size based pair-wise correlations for parental care activity and energetics for all fish nested within species

Pairwise correlations	r_s for total length		r_s for mass	
	Egg	Wriggler	Egg	Wriggler
Actual nest swim speed	NS(NS)	0.299(NS)	NS(NS)	0.268(NS)
Standardized nest swim speed	-0.565**(0.544)	-0.327(NS)	-0.478**(-0.494#)	-0.300(NS)
Standardized respiration	NS(NS)	0.353(NS)	NS(NS)	0.319(NS)
Actual respiration	0.925**(0.867*)	0.816**(0.799*)	0.943**(0.819)	0.849**(0.831#)
Energy expenditure	NS(NS)	-0.318*(-0.312#)	NS(NS)	-0.321*(-0.299#)

All correlations were conducted using Spearman's Test and only significant ($P < 0.05$) r_s values are provided. Values without an asterisk are significant at $P < 0.05$, * $P < 0.01$, ** $P < 0.001$. Phylogenetically independent contrasts (PIC) are in parentheses below absolute values. Marginally non-significant values ($P < 0.10$) for PICs are denoted by #. Sample sizes are available in Table 1. PIC values are $n-1$

stages (ANOVA: $F_{5,91} = 80.5$, $P < 0.001$; Fig. 2a). Respiration rates were highest for smallmouth bass and largemouth bass and lowest for pumpkinseed, bluegill, and black crappie. Respiration rates standardized for mass also differed among species for both egg (ANOVA: $F_{5,107} = 54.7$, $P < 0.001$) and wriggler stage (ANOVA: $F_{5,91} = 19.2$, $P < 0.001$) (Fig. 2c). Mass adjusted parental care per unit time was most costly for rock bass and smallmouth bass, and least costly for black crappie. In some cases, costs differed two-fold. For example, estimated respiration rates during the wriggler stage for bluegill were half those of smallmouth bass.

Overall energetic costs (estimated respiration rates summed over the entire period of parental care) differed among species. Significant species-specific differences were observed for standardized respiration (ANOVA: $F_{5,107} = 48682.2$, $P < 0.001$; Fig. 2d) and absolute respiration (ANOVA: $F_{5,107} = 142.5$, $P < 0.001$; Fig. 2b).

Significant positive correlations were found between the size of fish (both TL and mass; all Spearman correlations) and total absolute respiration during parental care (TL $r_s = 0.904$, $P = 0.001$, $r_{sPIC} = 0.851$, $P = 0.068$; mass $r_s = 0.865$, $P = 0.004$, $r_{sPIC} = 0.816$, $P = 0.092$; Fig. 3a, b), but not between size and total relative respiration.

Relationships between parental care and stage of offspring development

For some species, significant differences in swimming speeds were noted between egg and wriggler stages (t -tests: see Fig. 4). Consistent with our prediction, largemouth bass and smallmouth bass generally swam faster during the wriggler stage, whereas bluegill consistently had lower swimming speeds during the wriggler stage. Stage-specific patterns in respiration rates (energetic

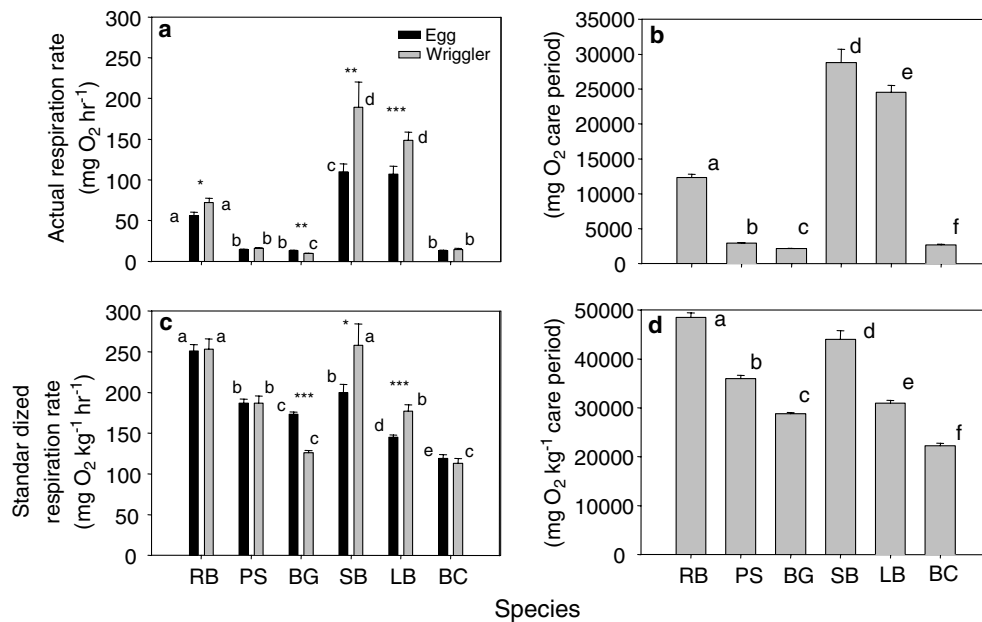


Fig. 2 Parental care energetics of six species of centrarchid fishes during (a, c) stage-specific development and (b, d) the entire parental care period (means \pm SE). For each species in panels a and c, the activity for the egg and wriggler stage was compared by two-sample t -tests. Stage-specific differences for each species are noted with asterisks. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Statistical

output is not provided for energy costs, but it mirrors the patterns of respiration. In panels b and d, one-way ANOVA, with the conservative Tukey-HSD test were used to evaluate differences ($P < 0.05$). For each panel, dissimilar letters indicate significant differences among species for respiration rate

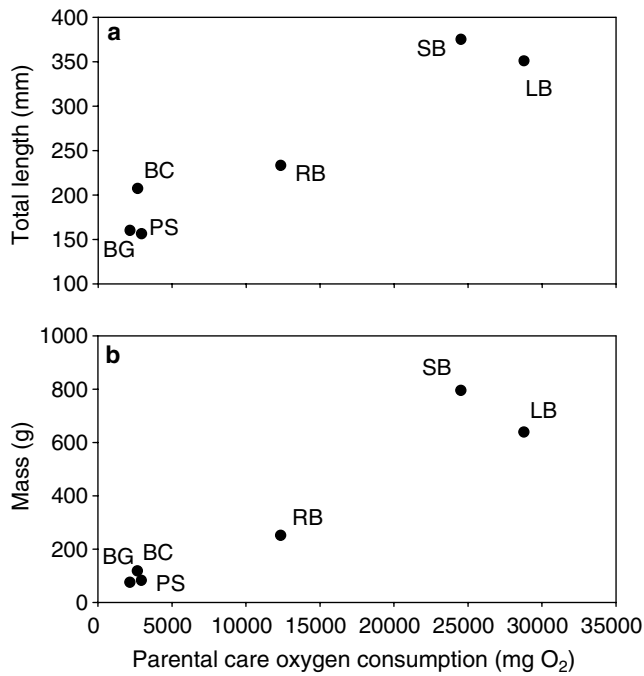


Fig. 3 Correlations between fish size (**a** total length, **b** mass) and total parental care oxygen consumption for six centrarchid species. Individual species abbreviations are noted on the figure

costs) generally followed the same patterns observed in swimming speeds for each species (*t*-tests: see Fig. 2a, b). Smallmouth bass and largemouth bass had higher respiration rates during the wriggler stage than during the

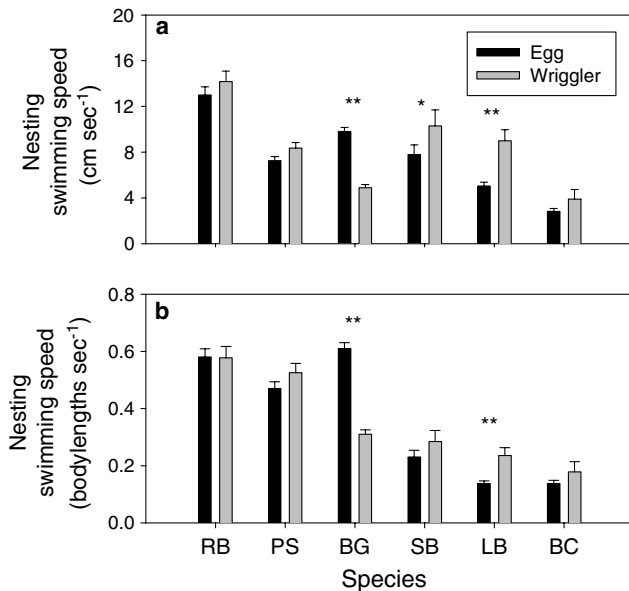


Fig. 4 Nesting swimming speeds of six species of centrarchid fishes providing parental care during the egg and wriggler stages of offspring development (means \pm SE). For each species, the activity was compared with each other by two-sample *t*-tests (* $P < 0.05$; ** $P < 0.001$)

egg stage. Conversely, bluegill respiration rates during the wriggler stage were roughly half those during the egg stage. Few differences were observed for stage-specific energetics in rock bass, pumpkinseed, and black crappie.

Relationships between parental care and egg size

Egg size (both mass and diameter) varied significantly among species (ANOVA: mass, $F_{5,89} = 2308.9$, $P < 0.001$; diameter, $F_{5,89} = 881.9$, $P < 0.001$; Table 1). When evaluated independently, several variables including duration of care (egg mass $R^2 = 0.808$, $P = 0.047$, $R^2_{\text{PIC}} = 0.781$, $P = 0.119$; egg diameter $R^2 = 0.785$, $P = 0.061$, $R^2_{\text{PIC}} = 0.697$, $P = 0.190$) and total energy expended (standardized for size of parental males) (egg mass $R^2 = 0.836$, $P = 0.038$, $R^2_{\text{PIC}} = 0.920$, $P = 0.027$; egg diameter $R^2 = 0.893$, $P = 0.016$, $R^2_{\text{PIC}} = 0.949$, $P = 0.014$) were correlated with egg size. Multiple regression provided a stronger model, however, and revealed that the best predictor of both egg diameter and egg mass was total energy expended (adjusted for size) during the parental care period. Energy expenditure increased with egg diameter (79.7% of variation) and egg mass (69.9% of variation), and to a lesser degree, the duration of parental care increased with egg diameter (15.4% of variation) and egg mass (22.7% of variation; multiple

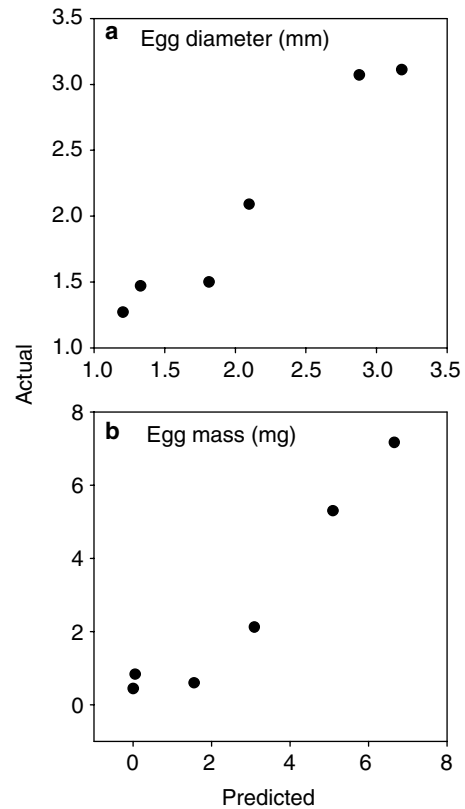


Fig. 5 Relationship between the multiple regression stepwise model prediction and **a** the actual egg diameter and **b** egg mass for six species of centrarchid fishes

regression: egg diameter, $R^2=0.952$, $F_{2,5}=29.6$, $P=0.011$; egg mass, $R^2=0.926$, $F_{2,5}=18.7$, $P=0.020$; Fig. 5a, b). No other parameters associated with parental care significantly improved the models.

Discussion

Relationships between parental care and parental body size

We observed substantial variation in parental care activity and energetics in six species of centrarchid fishes. Duration of care varied widely among species, ranging from several days in bluegill and pumpkinseed to several weeks for largemouth bass and smallmouth bass. Although duration of care varies among geographic locations due to environmental and other influences, our results are in general agreement with previous accounts (e.g., Breder 1936; Miller 1975; Gross and Nowell 1980; Colgan and Brown 1988). Using telemetry, we were able to follow parents after they left the nest to determine if they were continuing to provide care. The duration of care increased with the size of the species. Only largemouth bass and smallmouth bass were located with offspring after they left their nests. All our observations indicated that males provide exclusive care to the offspring. This includes largemouth bass, a species that was recently reported to have biparental care (DeWoody et al. 2000). Given that previous accounts of largemouth bass in northern latitudes indicated that parental care is provided exclusively by males (Breder 1936; Cooke et al. 2002), DeWoody et al. (2000) either discovered an unusual population or females in more southerly latitudes might assist with care.

For all analyses comparing reproductive attributes among species, we performed analyses with and without controlling for phylogeny. In all cases the two analyses were in close agreement, although in some cases significance was lost in the phylogenetically controlled analyses, primarily because sample sizes decreased from 6 to 5. Because effect sizes were similar in these cases, we consider these relationships significant. Previous studies have also documented that in some cases, PICs did not alter the findings observed using non-phylogenetically corrected data (e.g., Freckleton 2000; Frappell et al. 2001).

Average absolute swimming speeds of parental fish increased with fish size during the wriggler stage. Interestingly, however, when adjusted to the size of the species, across all stages, smaller species actually swam at relatively higher speeds than larger species, despite doing so at slower absolute speeds. This swimming represents both vigilance for predators and fanning activity (Blummer 1979). Larger species may have to be less vigilant because fewer predators may attempt to prey on their nests. However, largemouth bass and smallmouth bass, the two largest species, typically engage all potential predators and at greater distances than the

smaller species (Colgan and Brown 1988; Cooke et al. 2002), whereas the smaller species typically use more overt, less direct, tactics to deter predators (Colgan and Brown 1988; S.J. Cooke, unpublished data). Alternatively, the relatively high swimming speeds of smaller species may be a consequence of their smaller eggs requiring more fanning to keep them free of silt and supplied with oxygen (Coleman and Fischer 1991). In addition, smaller species with smaller eggs often have larger clutch sizes due to both the eggs being smaller (e.g., black crappie, pumpkinseed, bluegill; see Table 1) and to more frequent contribution of eggs by multiple females (e.g., pumpkinseed, bluegill). In addition, nest size and distribution of the offspring can also vary (e.g., Scott et al. 1997), but at present the role of these factors in energetic costs or reproductive success is poorly understood. As a result of increased swimming speeds associated with different levels of vigilance, fanning, and most importantly, differences in body size, absolute respiration rates and energy costs increased substantially with fish size. Size-adjusted respiration rates and energy costs still revealed a similar positive relationship with body size. Smaller fish were less efficient swimmers, expending more energy per unit distance than larger fish on a mass-specific basis. Collectively, the lower swimming efficiency of smaller species, coupled with their need to expend more energy fanning their nests, may limit the duration of parental care they can provide relative to larger species. Larger individuals within a species may also benefit from mating more (Wiegmann and Baylis 1995) and experiencing higher overwinter survival (Sullivan 1985). A study by Suski and Philipp (2004), however, suggested that it was fish of intermediate size that had the highest reproductive success and were the most vigilant parents.

In addition to examining instantaneous or rate-based patterns of parental care and energetics, we were able to use our empirically derived data on duration of care to estimate the total cost of parental care for each of the six species. When standardized to a mass of 1 kg, total respiration rates (Fig. 2b) and total energy costs (Fig. 2d) of parental care differed among species. However, no clear size-based patterns were evident. Because standard metabolic rate is negatively correlated with body size in fish (Schmidt-Nielsen 1984), variation in energy costs in addition to standard metabolic rate must be both substantial, and uncorrelated with body size across species, for this pattern to occur. Care was most expensive per unit mass for rock bass and smallmouth bass, and least costly for black crappie. When adjusted to the actual size of the fish, costs of parental care changed. Parental care provided by smallmouth bass and largemouth bass was clearly more costly than for the other species we examined. For these data, there was a strong positive relationship between the size of fish and total parental care respiration rates. To our knowledge, these data represent the first attempt to ascribe a cost to the entire parental care period for fish.

Relationships between parental care and stage of offspring development

We examined how intensity of parental care varied as offspring developed from egg to wriggler stage for fish with different durations of parental care. Consistent with our prediction, species with shorter duration care (pumpkinseed and black crappie) exhibited relatively stable patterns of parental care activity between the egg and wriggler stage. This pattern is not consistent with the prediction that parents should adjust care based on current and future reproduction (Trivers 1972), or with previous empirical assessments for these species (Colgan and Gross 1977; Colgan and Brown 1988). However, those empirical assessments of that theory for pumpkinseed and black crappie (i.e., Colgan and Gross 1977; Colgan and Brown 1988), both used attack distance in response to staged predator intrusions to document alterations in parental investment, not the suite of all possible behaviors or energetic costs that are also linked to current and future reproduction. Indeed, when Cooke et al. (2002) characterized a number of energetic correlates of parental care activity for smallmouth bass and largemouth bass, only some of the metrics they examined conformed with theory.

The most complete information on investment comes from our energetic data. These data are consistent with our prediction that when care is of short duration, energy expenditure would be similar among stages of offspring development. We also predicted that, despite having relatively brief individual bouts of parental care, bluegill would be more likely to conform with theory because males participate in multiple bouts of parental care over a single season (Coleman et al. 1985; Coleman and Fischer 1991). Thus, male bluegills must conserve energy during a given bout if they are to participate in future bouts. Consistent with this prediction, bluegill decreased energy expenditure between the egg and wriggler stage. Proximate factors contributing to this decrease in energetic expenditure between stages may include reductions in axial turning, pectoral fin rates, caudal fin rates, and nest swimming speeds. Furthermore, during the wriggler stage, some species were more likely to use display behaviors to deter predators, despite the fact that attempted predation rates were fewer, but successful predation rates were similar across stages (S.J. Cooke, unpublished data). Collectively, these data suggest that investment decreased for bluegill as offspring developed from egg to wriggler stage. Smallmouth bass, largemouth bass, and to a lesser extent, rock bass, were predicted to increase care during the wriggler stage, and our data generally supported this prediction. To conform with theory, this increase at the wriggler stage would be followed by a reduction in care as offspring continue to develop in species that provide extended care. This pattern has been observed for rock bass (Colgan and Brown 1988), smallmouth bass (Ridgway 1988; Cooke et al. 2002) and largemouth bass (Cooke et al. 2002). The natural history and behavior of the

offspring may also play a role in the elevated activity of larger species during the wriggler stage. As smallmouth bass offspring (and largemouth bass; S.J. Cooke, personal observations) develop, brood dispersion increases, both increasing the visibility of the offspring to predators and increasing the area that must be patrolled by parents (Friesen and Ridgway 2000). Conversely, offspring of the other four species we studied stay very close to the nest until they disperse during a brief period coinciding with the termination of parental care and male nest abandonment (S.J. Cooke, unpublished data).

The premise of our predictions regarding parental care intensity was that fish with short duration care would not alter intensity because they could afford to provide energetically costly care for short periods. By contrast, fish with long duration care are forced to budget energy expenditure and thus should vary their investment with both the value of the current brood relative to the value of future reproduction, and with the value of the care to the brood. Bluegill appear to be the exception that proves this rule, because they provide parental care of short duration, but as potential multiple spawners (Coleman and Fischer 1991) they must budget energy expenditure within breeding bouts. Repeat spawning may be possible for all of the species we examined, but this seems likely to occur only in instances where the brood was destroyed in early stages of development (Eipper 1975). Because all of our bluegill data were collected during earlier bouts of spawning, we do not know whether this pattern of energy budgeting occurs across all bouts.

Relationships between parental care and egg size

We developed stepwise multiple regression models that predicted up to 96% of observed variation in egg size among species. We predicted that the relationship between parental care and egg size should be more closely related to the energetics of parental care than to the duration of care. Indeed, although duration of care was an important contributor to the variation we observed, the most important contributor was the total energetic cost of care. More than two-thirds of the variation explained by our model was attributable to energetics, and the remaining third was attributable to duration. Because larger eggs should take longer to develop, they require extended parental care and thus increased parental energetic expenditure. Given the association between body size and energy reserves, even with energy budgeting, small species may not be able to afford the energy costs that caring for large eggs requires, which could account for the positive association between egg size and body size.

Sargent et al. (1987) assessed the relationship between egg size and parental care using duration of care as an indicator of quality. They included data on seven species of centrarchids, although all the Lepomids were grouped for analysis. The authors also included Sacramento

perch, *Archoplites interruptus*, a species at the extreme of the continuum, having the smallest eggs of the centrarchid family and virtually no care. We found the same relationship between duration of parental care and egg size. Our results suggest, however, that energy expenditure, independent of the duration of care, contributes to variation observed in egg size (or vice versa). Few models of parental care have incorporated the energetic cost of care to parents. In commenting on studies by Nussbaum (1985), Shine (1989) noted that Nussbaum's models did not consider the costs of parental care in terms of the energy budget or survival of the parent. Because these costs increase with the duration of care (as was evident in our study), which in turn is positively correlated with egg size, Shine (1989) suggested that energetic costs could prevent the evolution of parental care in species with large eggs. There is no doubt that increased duration of care does translate to increased cost, and it is this cost of care that was strongly correlated with egg size in our study. Given this expense to the parent, the benefit of caring for larger eggs must outweigh the costs. Smallmouth bass and largemouth bass benefit by producing larger offspring that can grow faster while the parent protects them from predation, delaying the development of predator avoidance tactics until parental care terminates (e.g., Brown 1985). Centrarchid fish with smaller eggs and shorter care can either spawn multiple times in a season (e.g., bluegill) but provide low levels of care, or provide short duration, but high intensity care such as what we observed for black crappie, pumpkinseed, and rock bass. By maintaining high intensity care, these species can provide maximal benefit to the existing brood, but terminate care before substantially compromising their own survival (Webb et al. 2002). In rock bass, the percent mass change during care affects over-winter survival of adults, illustrating the importance of energetics in determining the costs and benefits of different tactics (Sabat 1994). Despite the clear links between egg size and energetics and duration of parental care, more information about the ecology of larval fish is required to understand the factors that favor different egg sizes. Furthermore, we did not assess the number of eggs in each nest, which is also an important determinant of reproductive success, and thus of the trade-offs between egg size, fecundity, developmental rates, body size, and duration of care (Kolm and Ahnesjo 2005).

Conclusions

Recent reviews have noted the need to increase our understanding of the energetics of parental investment, especially with regard to fish (Sargent 1997). Some empirical studies, including this one, have examined the trade-offs that are mediated through energetics; however, the physiological basis for these trade-offs is poorly understood (Sargent 1997). Ridgway and Shuter (1994) found that changes in energy budgets can affect both

current and future reproduction. However, changes in energy budgets may result in a cost to other fitness components. Annual variation in resources, and environmental or social factors, can influence the energetics of reproduction and result in dynamic changes in reproduction from year to year. Future studies of parental care will benefit from determining the metabolic rates of animals in situ, rather than relying on short periods of video collection (Butler 1989; Cooke et al. 2002, 2004), as well as documenting other physiological information (e.g., Guderley and Guevara 1998). Because hormones can also contribute to elevated metabolic rates during the reproductive period (Burns 1975), future research should focus on combining measurements of locomotor activity with real-time indicators of metabolic rate such as heart rate. Current approaches that rely on just locomotor indices to estimate metabolic rate may be underestimating the costs of parental care. For centrarchids, the winter (e.g., Sullivan 1985) and the reproductive period (e.g., Hinch and Collins 1991; Cooke et al. 2002) have repeatedly been identified as the most stressful and potentially important periods regulating population size. Future assessments that attempt to link seasonal energetics with reproduction will be essential for understanding the plasticity of behaviors and in ascribing costs. Indeed, bioenergetics models rarely consider the reproductive period due to the lack of available input parameters, despite the fact that it is recognized as an energetically expensive component of the annual energy budget (Ney 1993). This paper provides some of the first reliable data on the reproductive energetics of centrarchid fishes that can serve as the basis for future studies on the comparative behavior and energetics of parental care in fishes. It is important to note, however, that although energy is clearly an important determinant of parental care behavior, it is not the only determinant. In our analyses, we focused our efforts on that topic because it has been largely ignored or not examined in a comparative manner. Future work building upon our research will hopefully attempt to address the broader life history and life-time energetic implications of parental care. Longer-term studies that follow individuals through their reproductive lifetime are required to better understand the role of body size and energetics on fitness. For example, even though we can obtain information on life-history traits such as longevity or age at maturation from the literature, we have no idea about the lifetime reproductive activities of individual fish (except see work by Raffetto et al. 1990; Wiegmann et al. 1992) and are therefore limited in how these data can be used. Longer-term studies of individual fish in closed populations (see Raffetto et al. 1990) is a necessity to explore further questions on the interplay between energetics, immediate reproductive success, and fitness. The types of data we collected here can also be incorporated into theoretical models to understand parental investment trade-offs (as has recently been done by Webb et al. 2002) or the relationship between egg size and quality of parental care.

We also identified one general pattern and relationship that is worthy of exploration using other animal models. Our findings suggest that, for capital breeders, the trade-offs between costs and benefits of parental care will be more pronounced the longer the duration of parental care. Conversely, for noncapital breeders that can acquire resources while providing parental care, the trade-offs should be less pronounced. Although this generalization seems reasonable, there are a number of empirical inconsistencies among other taxa such as passerine birds. Passerines (which are noncapital breeders) exhibit pronounced trade-offs (Andersson et al. 1981; Montgomerie and Weatherhead 1988), indicating an apparent failure of this general prediction. This prediction requires further evaluation across broader taxonomic groups, and more accurate estimates of both costs and benefits.

Acknowledgements This work was approved by the animal care committees at the University of Illinois and Queen's University. The Ontario Ministry of Natural Resources provided necessary permits. We gratefully acknowledge the staff of the Queen's University Biological Station, and in particular, Frank Phelan, for facilitating this work. Expert field assistance was provided by Kate Deters, Jack Degner, Emily Grant, Brandon Barthel, Deanna Barthel, Julie Claussen, Mickey Philipp, Madison Philipp, Maggie Bartkowska, Brian Jackson, Jenny Konrath, Jana Svec, Cory Suski, and Mike Siepker. Jenny Konrath also carefully transcribed data from the video recordings. Discussions with Scott Hinch facilitated analyses of videographic data. Comments provided by Dick Warner greatly improved the manuscript. Ted Garland kindly provided an updated version of software for PICs. Funding for this project was provided by a University of Illinois Research Board Grant to S.J.C. and D.P.P., a Natural Sciences and Engineering Research Council of Canada Fellowship to S.J.C., and a University of Illinois Program in Ecology and Evolutionary Biology Research Grant to S.J.C. Final preparation of the manuscript was supported by the University of British Columbia and Carleton University.

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