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Increased parental care cost for nest-guarding fish in a lake with hyperabundant nest predators

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Although parental care increases offspring survival, providing care is costly, reducing parental growth and survival and, thereby, compromising future reproductive success. To determine if an exotic benthic predator might be affecting parental care by nest-guarding smallmouth bass (*Micropterus dolomieu*), we compared nest-guarding behavior and energy expenditures in two systems, one with a hyperabundant recently introduced predator, the round goby (*Neogobius melanostomus*). In Lake Erie, USA, smallmouth bass vigorously defended their nests from benthic round gobies. In Lake Opeongo, Canada, smallmouth bass were exposed to fewer and predominantly open-water predators and were less active in their nest defense. From scuba and video observations, we documented that nest-guarding smallmouth bass chased predators (99% of which were round gobies) nine times more frequently in Lake Erie than in Lake Opeongo. This heightened activity resulted in a significant decline in weight and energetic content of guarding males in Lake Erie but no change in Lake Opeongo males. Bioenergetic simulations revealed that parental care increased smallmouth bass standard metabolic rate by 210% in Lake Erie but only by 28% in Lake Opeongo. As energy reserves declined and offspring became increasingly independent, males in both lakes consumed more prey and spent more time foraging away from their nests; however, nest-guarding smallmouth bass consumed few prey and, in Lake Erie, rarely consumed round gobies. Therefore, increased parental care costs owing to the presence of round gobies could affect future growth, reproduction, and survival if smallmouth bass approach critically low energy reserves. Key words: bioenergetics, exotic species, nest defense, parental care, round goby, smallmouth bass.

Many organisms provide parental care for their offspring because as investment in parental care increases, so does the probability that offspring survive (Sargent, 1988). Providing care is energetically costly, and therefore, the amount of parental effort reflects a balance between conflicting energetic demands of offspring (current reproduction) and maintenance of parental energetic condition for future reproduction (Tolonen and Korpimäki, 1996; Wiehn and Korpimäki, 1997; Williams, 1966). Providing care reduces energy reserves (Horak et al., 1999), reducing survival (Sabat, 1994), increasing time to next reproduction (Smith and Wootton, 1994), and reducing future fecundity (Balshine-Earn, 1995). Therefore, understanding parental care costs and parental behavior in response to brood value and parental condition is essential for our knowledge of reproductive systems.

Energetic cost of parental care varies greatly and depends on abiotic and biotic factors. When conditions demand more care (e.g., ambient temperature requires warming or oxygenation of offspring), parents expend more energy caring for their brood than when conditions are favorable (Coleman and Fischer, 1991; Skolbekken and Utne-Palm, 2001; Wiehn and Korpimäki, 1997). In addition, parents must increase nest-defense behaviors when nest predators

are abundant (Ghalambor and Martin, 2002; Popiel et al., 1996) or risk losing offspring. Increased parental aggression depletes energy reserves (Chellappa and Huntingford, 1989) and, ultimately, may lead to brood abandonment if a parent falls below a low-condition threshold (Horak et al., 1999). Although some studies have compared parental behavior across different environments (Ghalambor and Martin, 2000, 2002; Townshend and Wootton, 1985), few studies have evaluated how in situ environmental conditions affect the energetic cost of parental care.

We sought to assess parental behavior and parental care costs in a nest-guarding fish, the smallmouth bass (*Micropterus dolomieu*), in two populations, one population was exposed to a hyperabundant nest predator. Male smallmouth bass provide sole parental care for their offspring, constantly circulating water over their offspring and defending their brood from predators (Ridgway, 1988; Ridgway and Shuter, 1994). Care increases energetic costs (Gillooly and Baylis, 1999; Mackereth et al., 1999) by raising active metabolic rate up to 50% higher than that of individuals not providing care (Hinch and Collins, 1991) and by reducing feeding opportunities (Ridgway and Shuter, 1994). Parental care costs are amplified because males rarely leave their brood to forage and foraging range is reduced (Mackereth et al., 1999). As a result, male smallmouth bass lose energy during nesting (Gillooly and Baylis, 1999; Mackereth et al., 1999).

We measured the cost of parental care for smallmouth bass facing different risks of nest predation. In Lake Erie, Ohio, USA, smallmouth bass faced a high risk of nest predation from a recent invader and hyperabundant nest predator, the round goby (*Neogobius melanostomus*), which arrived in Lake Erie in 1993 (Charlebois et al., 1997). Because round gobies occur in high densities in Lake Erie (at times more than 100 round gobies/m²; Charlebois et al., 1997) and enter unguarded nests quickly when males are removed from nests (Steinhart et al., 2004), the risk to smallmouth bass offspring is compounded by potential changes in parental care behavior. We contrasted Lake Erie with Lake Opeongo, Ontario, Canada, where smallmouth bass experienced much lower predation risk. We hypothesized that male smallmouth bass that faced high nest-predation risk would exhibit more aggressive and defensive behaviors while guarding their offspring than would males exposed to low nest-predation risk. Further, aggressive males (i.e., those facing high nest-predator densities) should expend more energy than less aggressive males. Males may, however, compensate for energy expended on care by foraging more frequently. We hypothesized that male smallmouth bass may ameliorate the cost of brood defense against round goby by consuming this abundant fish. Whereas increased consumption may compensate for some costs of parental care (Ridgway and Shuter, 1994), foraging also reduces time spent on parental care (Townshend and Wootton, 1985), leading to offspring being more vulnerable to predators while the parent forages.

METHODS

Study species and sites

After spawning, in smallmouth bass, the parental male remains to guard developing offspring as the young pass through several developmental stages. As embryos, smallmouth bass are nonmobile and therefore extremely vulnerable to nest predators. Even after the offspring develop into free-swimming larvae and juveniles, the male continues to protect his brood 24 h a day for as long as 6 weeks (Coble, 1975). Herein, we considered male parental behavior at three stages of offspring development: unhatched embryos, hatched embryos, and free-swimming juveniles.

We observed and sampled nesting smallmouth bass in Lake Erie and Lake Opeongo. In

mesotrophic Lake Erie, we surveyed smallmouth bass using scuba in the Bass Islands, located in the western basin of Lake Erie (41° 40' N, 82° 50' W) during May and June 1999-2000. Sampled nests were in water 2-4 m deep over cobble with a cohesive clay base, where round gobies also were abundant (Steinhart et al., 2004). In oligotrophic Lake Opeongo (45° 42' N, 78° 22' W, Algonquin Park, Ontario), we observed nesting smallmouth bass via snorkeling during June 2001. Sampled nests were at 1-2-m depth on cobble. Round gobies were not present in Lake Opeongo during this research.

Nest-guarding behavior

In both lakes, divers or snorkelers located, observed, and videotaped nest-guarding males' nests between 0900 and 1600 h (exact times were selected haphazardly). We observed and videotaped parental behavior with a SeaViewer model 550 underwater, black and white video camera connected to a TV/ VCR combination. After the camera, mounted on a 0.5-m tripod, was placed within 0.5 m of the nest, the divers left the water, and we waited for 10 min before recording at least 15 min of smallmouth bass nest-guarding behavior. Once nests contained free-swimming young, the offspring and attending parent often would swim beyond the camera's view; hence, we analyzed parental behavior only for nests containing unhatched (i.e., fertilized eggs; 18 males in Lake Erie and 14 males in Lake Opeongo) and hatched embryos (22 males in Lake Erie and 13 males in Lake Opeongo).

We analyzed videotaped parental behavior using Beast Professional (Version 1.0J; G. Losey, University of Hawaii), a program for real-time recording and analysis of behavioral data. All video recordings were previewed to assign behaviors (by agreement between two observers) to one of two categories: "chase" or "departure." For 15 min of nest defense, we recorded the timing and duration of these behaviors in real time using Beast™. The behaviors were defined as given below.

Chase

Guarding male rapidly departed from or returned to the nest with quick, powerful tail beats. We included a rapid return to the nest as a chase because divers occasionally observed males slowly leaving the nest to investigate a potential threat and if a threat was ultimately chased, the males then returned to the nest very quickly. Additional behaviors indicative of a chase included (1) sudden orientation to a potential threat; (2) jawing, yawning, or fin displays (Ridgway, 1988), common when nest-guarding males are threatened; or (3) swimming toward an organism visible to the camera.

Departure

The guarding male slowly swam from the nest without any visual display of aggression. We assumed that chases were aggressive behaviors directed toward potential nest predators, but the function of departures was unclear. We summed total time spent away from the nest during chases and departures, then calculated percent time away from the nest. We used general linear models to examine how independent variables, male total length (TL), lake, offspring stage, and the lake-by-offspring stage interaction, affected frequency of chases and departures and the percent time away from the nest. Because predators were not always in camera view, we recorded chase orientation to provide insight into what predator (i.e., benthic or water column) was chased. We recorded the direction of each chase as up (>10° above horizon), down (<10° below horizon), or horizontal and compared chase orientation between the lakes with a chi-

square test ($\alpha = .05$ in all analyses). We assumed down-oriented ($>10^\circ$ below horizontal) chases were for pursuing benthic predators (e.g., round gobies in Lake Erie), while horizontal and up-oriented ($>10^\circ$ above horizontal) chases were for pursuing predators in the water column.

Parent condition and energy density

We measured condition and energy density of male smallmouth bass early in parental care, when males were guarding unhatched embryos (19 males in Lake Erie and 12 males in Lake Opeongo), and late in care, when males were guarding free-swimming juveniles (20 males in Lake Erie and 13 males in Lake Opeongo). In Lake Erie, scuba divers used a rod and reel or a landing net to remove nest-guarding males. In Lake Opeongo, males were angled from nests from shore or a boat. In both lakes, males were selected haphazardly but did represent the size range in each population. Captured males were euthanized in a mixture of MS222 and lake water, placed on ice, and within 1 h of capture, frozen in water in airtight bags at 10°C for 1-5 months.

After thawing, we weighed (± 0.01 g, wet weight [WW]) and measured (± 1 mm, TL) each fish and removed its digestive tract. Tract contents were removed and stored in 95% EtOH. We separated testes from other viscera, setting both aside for energy density measurements. To test if a small tissue sample could accurately predict whole-body energy density, we used a 5-mm-diam dermal punch to remove two small tissue samples (mean = 0.8 g), one from each lateral side below the dorsal fin, from each smallmouth bass. The remaining carcass was cut into pieces smaller than 100 cm^3 . Each tissue type (testes, viscera including emptied digestive tract, tissue plugs, body) was weighed and then dried at 60°C to constant weight ($\pm 1\%$, usually 24-96 h). Next, testes, viscera, and tissue plugs were ground with a mortar and pestle, whereas the body was ground in a Retsch grinder. Ground samples then were dried an additional 24 h. We measured caloric density of the body tissue with a Parr Bomb Calorimeter (Model 1672) and of the testes, viscera, and tissue plugs with a Parr Semi-micro Calorimeter (Model 1425). Bomb calorimeters measure the heat released from combusting the enclosed sample (e.g., lipids and protein), leaving behind only ash. We calculated caloric density (kJ/g WW) for each tissue and total energetic content (kJ) for each tissue by multiplying the weight of each tissue type by its caloric density. Whole-body energy content was calculated by summing the energy content of all tissue types and whole-body energy density as the weighted average (by WW) of energy density for each tissue.

Because energy density can be influenced by fish size (Mackereth et al., 1999), we used the residuals of WW and energetic content (in kilojoules in viscera, testes, or whole body) from regressions on TL in all analyses (Steinhart and Wurtsbaugh, 2003; Sutton et al., 2000). We used general linear models to explore how residuals of parent WW and energetic content (kJ) varied by TL, lake (Erie and Opeongo), offspring stage (embryo and juvenile), and the lake-by-offspring stage interaction. We used individual contrasts to compare male whole-body energetic content between lakes for males guarding embryos and males guarding juveniles. We used linear regression to test if whole-body energy density was related to tissue plug energy density.

Diet of guarding males

After removing the contents of the digestive tract, all prey larger than 5 mm were identified under a dissecting microscope and placed into one of three categories: fish, macro-invertebrates, or crayfish. Fish were identified to species using vertebral counts when necessary (Becker, 1983; Trautman, 1981). Each prey item was dried at 60°C to constant weight ($\pm 1\%$,

typically 24 h). From these data, we estimated daily ration by using the Eggers model to correct for gut evacuation rate over 24 h (Eggers, 1977):

$$\text{Daily ration} = \text{weight of prey in stomach} \times \text{evacuation rate} \times \text{hours}$$

where the evacuation rate was estimated as 0.1 (Rogers and Burley, 1991) and hours = 24 h because samples were collected daily. The Eggers model is a reasonable estimate of daily ration (Boisclair and Leggett, 1988). Daily ration was converted to mass-specific ration by dividing by male smallmouth bass weight. The relationship between daily ration (g/day) at the start of parental care (i.e., males guarding embryos) and at the end of care (i.e., males guarding juveniles) in each lake was explored with a general linear model, with daily ration as the dependent variable and lake (Erie and Opeongo), offspring developmental stage (embryo and juvenile), and the lake-by-offspring stage interaction as independent variables. We used individual contrasts to ask when daily consumption differed with offspring stage within each lake.

Bioenergetic simulations

We used a bioenergetic model (Hanson et al., 1997) to estimate the metabolic rate, or activity level (ACT), of nest-guarding smallmouth bass in Lakes Erie and Opeongo. The model predicted end weight (i.e., end parental care, 30 June in both lakes) based on observed WW of males at the start of parental care (i.e., males guarding unhatched embryos, 13 June in Lake Erie and 11 June in Lake Opeongo), energy density at the start and end of the parental care, total consumption (g), and diet composition of nest-guarding smallmouth bass, in addition to prey energy density and water temperature (Table 1). For each lake, we used regressions to estimate the WW and energy density of an average-length smallmouth bass at the start and at the end of parental care from the observed mean TL.

After running simulations with the base metabolic parameters established for adult smallmouth bass (Whitledge et al., 2003), we adjusted the ACT in the model until the model results produced the final WW matching the mean male WW measured at the end of parental care (± 1 g). The ACT parameter is a constant that is multiplied by standard metabolic rate (i.e., for the standard metabolism of an average adult smallmouth bass, ACT = 1; Whitledge et al., 2003). Increasing ACT simulates changes in respiration due to the increased activity associated with swimming and chasing predators. We used lake-specific estimates of ACT in calculations of net energy expended on parental care. We first estimated the net amount of energy expended on care by calculating the total change in energy content of males from start to finish of parental care plus the total consumption during that time. From this, we subtracted the net change in energy under the assumption that ACT = 1 (i.e., the energetic cost of standard metabolic activities for the simulation period).

Table 1

Parameters used in the bioenergetic model (Hanson et al., 1997) to determine ACTs, which produced observed changes in weight and energy density of male nest-guarding smallmouth bass in Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada

Model parameter	Lake Erie	Lake Opeongo
Simulation length (day)	17	19
Total prey consumption by smallmouth bass (g)	34	55
Percent fish in diet	60	55
Percent invertebrates in diet	40	45
Smallmouth bass starting WW (g)	852	585
Smallmouth bass ending WW (g)	754	571
Smallmouth bass starting energy density (kJ/g)	6004	4949
Smallmouth bass ending energy density (kJ/g)	5355	4831

Smallmouth bass WW (g), energy density (kJ/g of WW), duration of parental care (simulation length), and diet (composition and gram of prey consumed for the entire simulation length) are from field measurements (Lake Erie, $N = 39$ fish; Lake Opeongo, $N = 25$ fish). Temperatures for the simulations derived from three temperature loggers placed near nests in each lake during nesting. Prey energy densities (6000 kJ/g for fish and 4000 kJ/g for macroinvertebrates) were estimated for a composite of species (Hanson et al., 1997). We used the same consumption, respiration, and egestion/excretion parameters for adult smallmouth bass (Whitledge et al., 2003), regardless of lake.

Differences in net energy costs of parental care between Lake Erie and Lake Opeongo could potentially be the result of differences between the lakes in temperature, consumption, or ACT. To test how ACT alone influenced final total energetic cost of guarding nests, we used the Lake Erie ACT (associated with the presence of round gobies) in a simulation of nest-guarding males in Lake Opeongo, with all other Lake Opeongo parameters held constant. In this way, we could isolate the influence of round goby-induced high ACTs on differences in costs of parental care in the two systems.

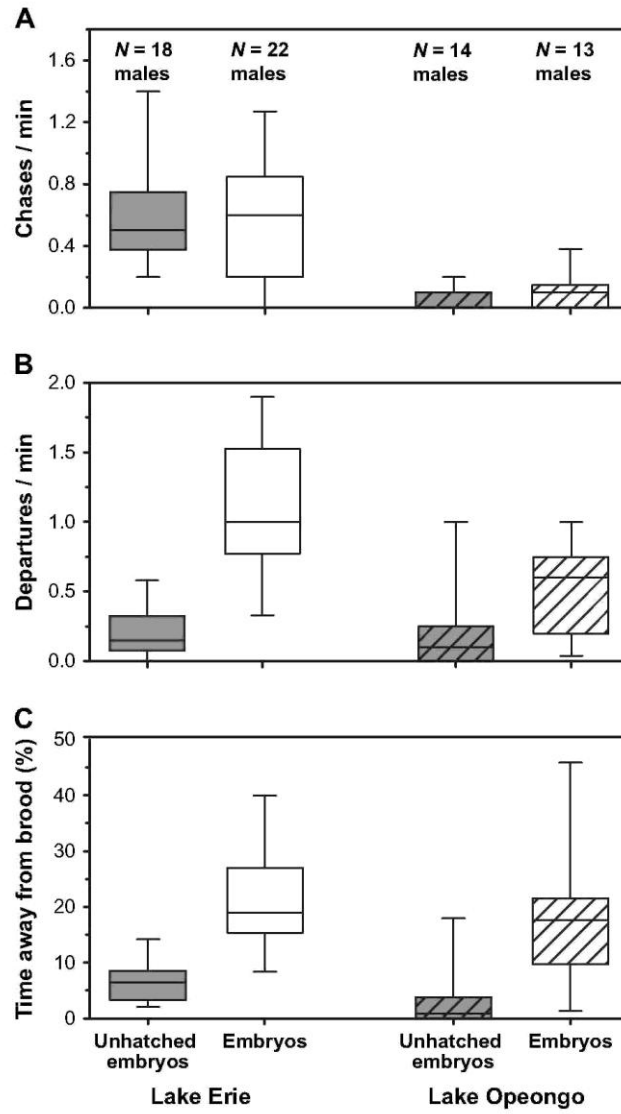


Figure 1

Nest-guarding behaviors for male smallmouth bass guarding un-hatched and hatched embryos in Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada. Chases (A) were rapid swimming motions to chase potential predators from a nest and were more frequent in Lake Erie than in Lake Opeongo (lake effect: $F_{1,63} = 45.99$, $p < .0001$). The purpose of departures was unknown, but both departure frequency (B; stage effect: $F_{1,63} = 28.78$, $p < .0001$) and percentage of total observation time spent away from the nest (C; stage effect: $F_{1,63} = 29.13$, $p < .0001$) increased after offspring hatched. Horizontal lines indicate the median values, box ends represent the 25th and 75th percentiles, and error bars represent the 10th and 90th percentiles.

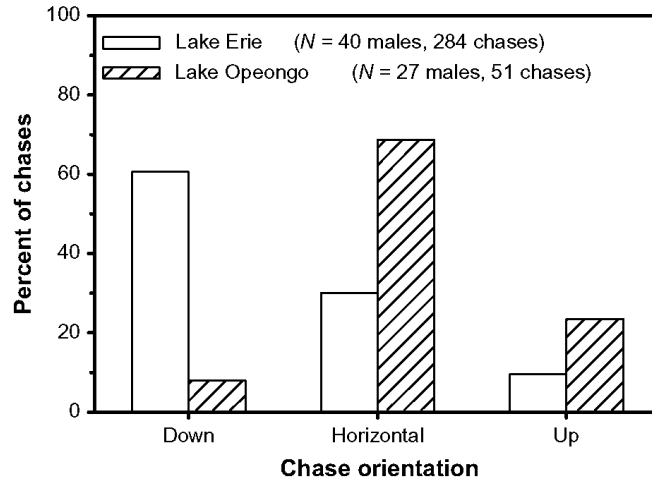


Figure 2

Orientation of chases made by male nest-guarding smallmouth bass in Lake Erie, Ohio, USA (1999 and 2000), and Lake Opeongo, Ontario, Canada (2001). Downward chases were more common in Lake Erie than in Lake Opeongo ($\chi^2 = 60.7$, $df = 2$, $p < .0001$).

RESULTS

Nest-guarding behavior

Male nest-guarding smallmouth bass in Lake Erie defended their nests more aggressively than males in Lake Opeongo. Male TL did not affect chase frequency ($F_{1,46} = 1.15$, $p = .29$). Because TL was not a significant factor and we had length measurements for only 51 males, we removed TL from the model to allow us to use our full sample size for these behaviors (67 males). Lake was the only variable that significantly influenced chase frequency ($F_{1,63} = 45.99$, $p < .0001$). Nest-guarding smallmouth bass in Lake Erie, regardless of offspring stage ($F_{1,63} = 0.04$, $p = .83$) or the lake-by-offspring stage interaction ($F_{1,63} = 0.25$, $p = .62$), chased predators nine times more frequently than smallmouth bass in Lake Opeongo (Figure 1).

Nest-guarding males in Lake Erie chased benthic predators more often than males in Lake Opeongo. Chase orientation by nest-guarding smallmouth bass differed significantly between these two lakes ($\chi^2 = 60.7$, $df = 2$, $p < .0001$). In Lake Erie, 61% of chases were benthic oriented, whereas in Lake Opeongo, horizontal chases were most common (68%; Figure 2). Because most chases were benthic oriented in Lake Erie and more than 99% of predators confirmed in videotapes were round gobies (Steinhart et al., 2004), we conclude that nearly all chases in Lake Erie were directed toward this introduced predator. In Lake Opeongo, observed predators were in the water column: smallmouth bass, yellow perch (*Perca flavescens*), and pumpkinseed (*Lepomis gibbosus*). Snorkelers observed only one benthic fish, a darter (*Ethostoma* or *Percina* spp.), in a smallmouth bass nest in Lake Opeongo.

Although nest-guarding smallmouth bass were more aggressive in Lake Erie than in Lake Opeongo, they left their brood more frequently after their embryos hatched (Figure 1). Departure frequency ($F_{1,46} = 2.95$, $p = .09$) and percent time away from the nest ($F_{1,46} = 0.37$, $p = .54$) were not significantly influenced by male TL, so we removed TL from these models. Lake ($F_{1,63} = 7.76$, $p = .01$), offspring stage ($F_{1,63} = 7.88$, $p = .01$), and their interaction ($F_{1,63} = 28.78$, $p < .0001$) all had significant effects on departure frequency, driven mostly by the high departure frequency of males guarding hatched embryos in Lake Erie. In both lakes, males spent

significantly more time away from the nest after their offspring hatched (Figure 1; lake: $F_{1,63} = 1.89$, $p = .19$; offspring stage: $F_{1,63} = 29.13$, $p < .001$; lake by stage: $F_{1,63} = 0.01$, $p = .92$).

Parent condition and energy density

In general, male condition and energy content, measured as residuals from population-specific regressions with TL, declined from the start (i.e., guarding unhatched embryos) to finish (i.e., guarding juveniles) of parental care (Figure 3). Large males lost significantly more WW and energetic content than small males in Lake Erie, but male size (TL) had no significant effect in Lake Opeongo (Figure 3; Table 2). Energy density of tissue plugs was associated with whole-body energetic density ($F_{1,61} = 7.52$, $p = .008$). Tissue plug energy density, however, explained only 11% of the variation in whole-body energetic density and underestimated whole-body energy density (slope $b_1 = 0.42$) as fat reserves are often stored in tissues (e.g., liver) not sampled by tissue plugs.

Residuals of WW and energy content of body and testes were all significantly influenced by offspring stage and the lake-by-offspring stage interaction (Table 3). Males in Lake Erie started with higher residual WW than males in Lake Opeongo ($F_{1,59} = 4.49$, $p = .038$) and lost significant residual WW while providing care ($F_{1,59} = 28.95$, $p < .0001$), while males in Lake Opeongo did not lose residual WW during care ($F_{1,59} = 1.12$, $p = .29$). When the combined energetic content of all tissues was compared, nest-guarding males in Lake Erie began with a significantly higher whole-body energy content than males in Lake Opeongo ($F_{1,59} = 9.41$, $p = .003$) and declined 11% in energetic content while providing care ($F_{1,59} = 45.36$, $p < .0001$). Nest-guarding males in Lake Opeongo did not decline significantly in energetic content ($F_{1,59} = 0.45$, $p = .51$). Energy content of the viscera did not explain the change in whole-body energetic content. Viscera energetic content did not change during parental care, although a decline was nearly significant in Lake Erie ($F_{1,59} = 3.63$, $p = .062$; Lake Opeongo: $F_{1,59} = 0.01$, $p = .91$). Energy content of testes declined significantly during care in both Lake Erie ($F_{1,59} = 51.12$, $p < .0001$) and Lake Opeongo ($F_{1,59} = 10.16$, $p = .002$), but the contribution of testes to the total energetic content was small (<1%).

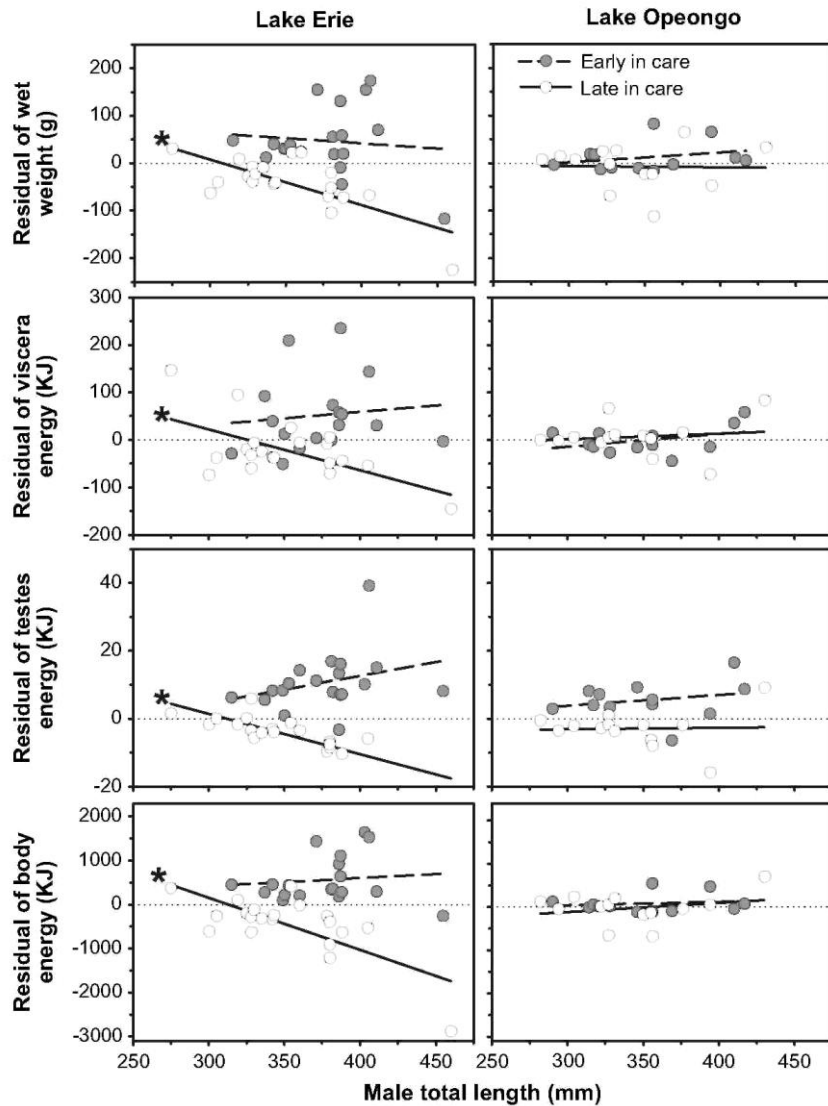


Figure 3

Residuals from regressions between male smallmouth bass TL and WW and between TL and body, viscera, and testes energy density (kJ/g) in Lake Erie, Ohio, USA (2000), and Lake Opeongo, Ontario, Canada (2001) plotted against TL. Data from early (i.e., males guarding embryos: 19 males in Lake Erie and 12 males in Lake Opeongo) and late parental care (i.e., males guarding juveniles: 20 males in Lake Erie and 13 males in Lake Opeongo) were pooled within each lake to calculate residuals, but residual regressions versus TL were performed separately for each period. Positive residuals indicate fish in better than average condition. Significant regressions are indicated with an asterisk (see Table 2 for regression results).

Diet of guarding males

More nest-guarding smallmouth bass had prey in their stomach in Lake Opeongo (64%) than in Lake Erie (21%). Only 3 of 39 guarding male smallmouth bass in Lake Erie ate round gobies. Although the trend was for higher consumption (in g) by males in Lake Opeongo than in Lake Erie, lake did not significantly affect mean daily consumption in our overall model ($F_{1,60} = 3.42$, $p = .069$). Offspring stage affected daily consumption ($F_{1,60} = 9.16$, $p = .036$): males

guarding juveniles consumed significantly more than males guarding embryos in both Lake Erie ($F_{1,60} = 2.29$, $p = .026$) and Lake Opeongo ($F_{1,60} = 2.05$, $p = .045$). In addition, percentage of males consuming prey increased from males guarding embryos (Lake Erie: 5%; Lake Opeongo: 50%) to males guarding juveniles (Lake Erie: 30%; Lake Opeongo: 77%). Daily consumption increased from start to finish of parental care and was negatively related to male energetic content (Figure 4).

Bioenergetic simulations

ACT of nest-guarding smallmouth bass increased above standard metabolism (ACT = 1) to match field changes in weight and energy density. In Lake Erie, bioenergetic simulations revealed that guarding males had an ACT of 3.1; in Lake Opeongo, males had an ACT of 1.2. Increased ACTs substantially influenced cost of parental care (Figure 5). Although longer males experienced higher parental care costs than small males, the differences were small compared to the effects of changing ACT. A 350-mm smallmouth bass in Lake Erie would spend 381 kJ providing parental care over 19 days. Lower ACTs in Lake Opeongo required that similar-sized males spent only 53 kJ over 17 days of care. After correcting for average number of days of care, male smallmouth bass in Lake Erie invested more than six times the energy per day than did males in Lake Opeongo. When male ACT in Lake Opeongo was raised to 3.1, cost of parental care was nearly identical to that in Lake Erie, with the difference the result of slightly higher metabolic costs associated with 1-2°C higher temperatures during parental care in Lake Opeongo than in Lake Erie.

Table 2

Individual regressions of residuals of WW and body, organ, and testes energy density versus TL for male smallmouth bass early in parental care (i.e., guarding embryos) or late in parental care (i.e., guarding free-swimming juveniles) in Lake Erie, Ohio, USA (2000), and Lake Opeongo, Ontario, Canada (2001; Figure 3)

	Variable	Lake Erie			Lake Opeongo		
		Slope	<i>t</i>	<i>p</i>	Slope	<i>t</i>	<i>p</i>
Early in care (guarding embryos)	WW	-0.22	-0.41	.69	0.21	0.86	.41
	Body energy	1.77	0.45	.66	0.79	0.47	.65
	Viscera energy	0.27	0.44	.67	0.27	1.30	.22
	Testes energy	0.08	1.32	.21	0.03	0.75	.47
Late in care (guarding juveniles)	WW	-0.96	-4.38	.001	-0.02	-0.07	.99
	Body energy	-11.85	-4.41	.001	2.13	0.84	.42
	Viscera energy	-0.86	-2.13	.01	0.12	0.43	.67
	Testes energy	-0.12	-6.81	<.001	0.01	0.12	.91

Slopes different from zero (bold results) reveal a significant effect of male length for that variable. Regression results were corrected for number of analyses ($\alpha = .003$).

DISCUSSION

Male smallmouth bass in Lake Erie spent more energy defending their offspring than males in Lake Opeongo, and the recent round goby invasion into Lake Erie appears related to high energetic expenditures and aggression. Nest-guarding smallmouth bass chased predators more than nine times as frequently in Lake Erie (with round gobies) than in Lake Opeongo

(without round gobies). Different predator communities in each lake make direct comparison imperfect, but several observations reveal that round gobies led to more aggressive nest defense. First, nesting smallmouth bass chase rates have increased about three-fold since round goby invaded (Goff, 1984). Second, predation risk, measured as cumulative number of seconds spent by all predators in a nest left unguarded for 2.5 min, was higher in Lake Erie (750 predator s; Steinhart et al., 2004) than in Lake Opeongo (0 predator s; Steinhart, unpublished data). Third, while we could not identify the object of chases by nest-guarding males, benthic-oriented chases were most common in Lake Erie, whereas upward-oriented chases were most common in Lake Opeongo. Given that round gobies are benthic fish lacking a swim bladder and more than 99% of nest predators in Lake Erie were round gobies (Steinhart et al., 2004), we conclude that round gobies were the object of the majority of chases and, thus, the dominant factor for different parental behaviors in Lakes Erie and Opeongo.

In Lake Erie, increased chase frequency raised nest-guarding smallmouth bass activity rates by up to 210% leading to loss of 20 kJ of energy per day of care provided. These values were higher than those reported for smallmouth bass where round gobies were not present (Cooke et al 2002). Although nest-guarding smallmouth bass in Lake Opeongo did not decline in either residual WW or whole body energetic content during our study, their activity rate were 28% higher than standard metabolism. In another study of nest-guarding smallmouth bass in Lake Opeongo, significant energetic declines were observed from start to finish of parental care (Mackereth et al., 1999). We may have failed to find a decline in energetic content during our Lake Opeongo study because males increased their consumption during care. Different experimental methods also might explain the different patterns in energetic content. Mackereth et al. (1999) extracted only lipids, ignoring the possibility that lipids may have been allocated to growth during parental care. Our method, measuring caloric density of different body components, included the energy stored in both lipids and proteins.

Table 3

General linear models of the factors affecting condition measures of male nest-guarding smallmouth bass in Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada

Variable	Source	<i>F</i>	<i>p</i>
WW (g)	Lake	0.01	.99
	Offspring stage	20.18	<.0001
	TL	3.07	.09
	Lake × stage	6.95	.01
Body (kJ)	Lake	0.42	.52
	Offspring stage	21.42	<.0001
	TL	4.14	.05
	Lake × stage	13.44	.001
Viscera (kJ)	Lake	0.01	.94
	Offspring stage	1.25	.27
	TL	1.50	.23
	Lake × stage	1.72	.19
Testes (kJ)	Lake	1.47	.23
	Offspring stage	48.19	<.0001
	TL	0.84	.36
	Lake × stage	4.47	.04

Condition measures were the residuals of WW and energetic content of tissues (body, viscera, and testes) derived from population-specific regressions versus smallmouth bass TL. Offspring stage is a surrogate for time in parental care (i.e., males guarded embryos early in care and juveniles late in care). Significant factors are indicated in bold and *df* = 1,59 for all tests.

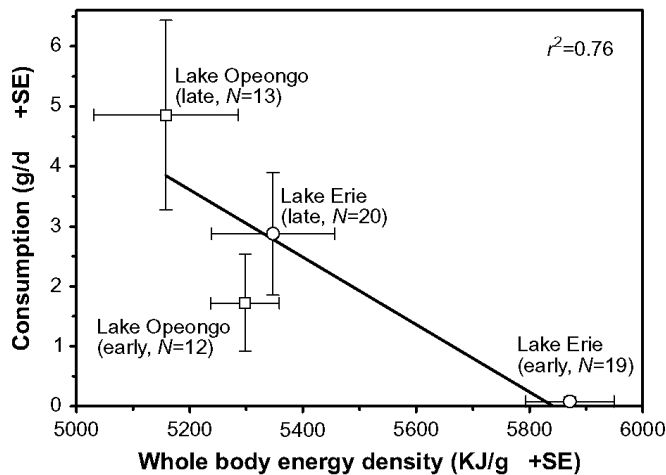


Figure 4
 Estimated daily consumption of prey (g/day) versus whole-body energy density of male nest-guarding smallmouth bass, early and late in parental care, in Lake Erie, Ohio, USA (2000), and Lake Opeongo, Ontario, Canada (2001). Both lake ($F_{1,60} = 4.08$, $p = .05$) and time (early or late in parental care; $F_{1,60} = 9.77$, $p = .003$) affected mean consumption.

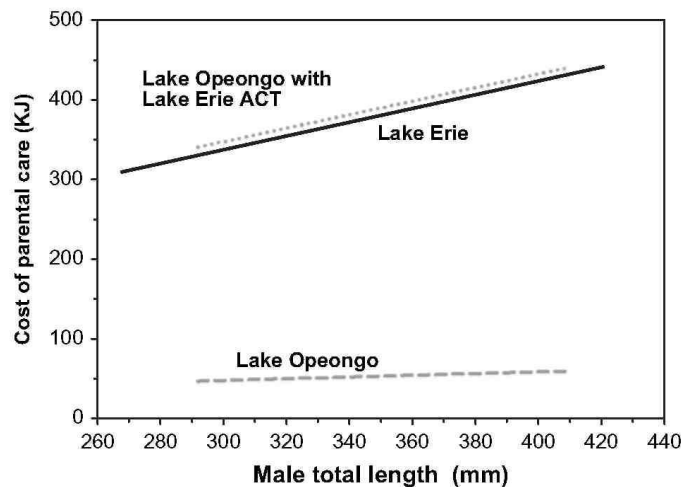


Figure 5
 Estimated direct costs of parental care from bioenergetic simulations of male nest-guarding smallmouth bass in Lake Erie, Ohio, USA (1999-2000, round gobies present), and Lake Opeongo, Ontario, Canada (2001, no round gobies), with expected costs if round gobies occurred in Lake Opeongo. To simulate the effects of round gobies in Lake Opeongo, ACT was raised to the level of smallmouth bass in Lake Erie. The cost of care plotted here resulted only from changes in ACT because we assumed constant consumption.

In both lakes, as the number of days spent guarding the brood increased, male energetic content declined and male daily consumption increased. Mackereth et al. (1999) also reported

feeding by nest-guarding males. Other organisms that provide parental care increase consumption as their energy reserves decline (Dearborn, 2001; Townshend and Wootton, 1985) and during stressful conditions (Pravosudov and Grubb, 1998). Other fish also increase consumption when their energy reserves are low (Metcalfe and Thorpe, 1992; Steinhart and Wurtsbaugh, 2003). When daily consumption increased, males increased departure frequency, spending more time away from their nests than when males were in better condition. Parental investment theory predicts that as the brood ages, it becomes more valuable, so parents should invest more heavily into caring for old broods than young broods (Östlund-Nilsson, 2002; Ridgway, 1988). But we observed that males spent less time caring for broods as offspring aged, possibly because guarding males increased their foraging frequency to augment energy reserves. Energy expenditures by parents can reduce future fitness (Balshine-Earn, 1995; Horak et al., 1999; Sabat, 1994; Smith and Wootton, 1994), but increasing consumption can, in part, compensate for energetic investments in parental care. Although males were not observed during departures, they may have been foraging, as suggested by their increased consumption. Time away from the nest also may have increased if chases and departures were of longer duration due to capture and handling time of prey. We observed these behavioral changes while offspring developed from un-hatched to hatched embryos. All smallmouth bass embryos are relatively nonmobile, so the decline in parental care occurred while the offspring still required the male to protect them from predators.

A reduction in brood size has been shown to decrease the ability or willingness of male smallmouth bass to guard their remaining offspring (Suski et al., 2003). In Lake Erie, round gobies quickly enter unguarded nests and consume between 400 and 2000 offspring within 5 min and can consume an entire brood in approximately 15 min (Steinhart et al., 2004). In addition, as parental condition declined and defending nests from round gobies accelerated this decline, males spent more time away from their nest. Round gobies may be able to seize these opportunities to consume offspring from unguarded nests. After round goby predation, reduced broods should receive less care and may be more likely to be abandoned by the nest-guarding male than large broods (Sargent, 1988; Suski et al., 2003; Townshend and Wootton, 1985). Round goby, therefore, compound the mortality risk to smallmouth bass offspring by direct predation and, presumably, by causing changes in parental care behavior.

Round goby, as an exotic predator, clearly has changed the behavior and cost of parental care for nest-guarding small-mouth bass in Lake Erie. But the significance of this finding stretches beyond smallmouth bass behavior as many species alter their parental behavior when faced with different predation risks (Ghalambor and Martin, 2000, 2002; Willson et al., 2001). Changes in parental behavior affect the amount of energy spent on parental care (Coleman and Fischer, 1991; Horak et al., 1999; Sabat, 1994). In turn, cost of care should affect parental decisions in the context of lifetime reproductive success (Ghalambor and Martin, 2000; Östlund-Nilsson, 2002; Popiel et al., 1996). Exotic species invasions are now common; therefore, we must consider how invaders may alter reproductive behavior and success of native species.

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REFERENCES

- Balshine-Earn S, 1995. The costs of parental care in Galilee St. Peter's fish, *Sarotherodon galilaeus*. *Anim Behav* 50:1-7.
- Becker GC, 1983. *Fishes of Wisconsin*. Madison, Wisconsin: University of Wisconsin Press.
- Boisclair D, Leggett WC, 1988. An *in situ* experimental evaluation of the Elliot and Persson and the Eggers models for estimating fish daily ration. *Can J Fish Aquat Sci* 45:138-145.
- Charlebois PM, Marsden EJ, Goettel RG, Wolfe RK, Jude DJ, Rudnika S, 1997. The round goby, *Neogobius melanostomus* (Pallas), a review of European and North American literature. Champaign, Illinois: Illinois-Indiana Sea Grant Program and Illinois Natural History Survey.
- Chellappa S, Huntingford FA, 1989. Depletion of energy reserves during reproductive aggression in male three-spined stickleback, *Gasterosteus aculeatus* L. *J Fish Biol* 35:315-316.
- Coble DW, 1975. Smallmouth bass. In: *Black bass biology and management* (Stroud RH, Clepper H, eds). Washington, D.C.: Sport Fishing Institute; 21-33.
- Coleman RM, Fischer RU, 1991. Brood size, male fanning effort and the energetics of a nonshareable parental investment in bluegill sunfish, *Lepomis macrochirus* (Teleostei: Centrarchidae). *Ethology* 87:177-188.
- Cooke SJ, Philipp DP, Weatherhead PJ, 2002. Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. *Can J Zool* 80:756-770.
- Dearborn DC, 2001. Body condition and retaliation in the parental effort decision of incubating frigatebirds (*Fregata minor*). *Behav Ecol* 12:200-206.
- Eggers DM, 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. *J Fish Res Board Can* 34:290-294.
- Ghalambor CK, Martin TE, 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Anim Behav* 60:263-267.
- Ghalambor CK, Martin TE, 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behav Ecol* 13:101-108.
- Gillooly JF, Baylis JR, 1999. Reproductive success and the energetic cost of parental care in male smallmouth bass. *J Fish Biol* 54:573-584.
- Goff G, 1984. The reproductive behaviour and ecology of smallmouth bass (*Micropterus dolomieu*) in Long Point Bay, Lake Erie (PhD dissertation). London, Ontario: The University of Western Ontario.
- Hanson PC, Johnson TB, Schindler DE, Kitchell JF, 1997. *Fish Bioenergetics 3.0*. Madison, Wisconsin: University of Wisconsin Sea Grant Institute.
- Hinch SG, Collins NC, 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observation. *Trans Am Fish Soc* 120:657-663.
- Horak P, Jenni-Eiermann S, Ots I, 1999. Do great tits (*Parus major*) starve to reproduce? *Oecologia* 119:293-299.
- Mackereth RW, Noakes DLG, Ridgway MS, 1999. Size-based variation in somatic energy reserves and parental care expenditure by male smallmouth bass, *Micropterus dolomieu*. *Environ Biol Fishes* 56:263-275.
- Metcalfe NB, Thorpe JE, 1992. Anorexia and defended energy levels in over-wintering juvenile salmon. *J Anim Ecol* 61:175-181.
- Östlund-Nilsson S, 2002. Does paternity or parental investment determine the level of parental care and does female choice explain egg stealing in the fifteen-spined stickleback? *Behav Ecol* 13:188-192.
- Popiel SA, Perez-Fuentetaja A, McQueen DJ, Collins NC, 1996. Determinants of nesting success in the pumpkinseed (*Lepomis gibbosus*): a comparison of two populations under different risks of predation. *Copeia* 1996:649-656.
- Pravosudov VV, Grubb TCJ, 1998. Management of fat reserves in tufted titmice *Baeolophus bicolor* in relation to

- risk of predation. *Anim Behav* 56:49-54.
- Ridgway MS, 1988. Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieu*). *Can J Zool* 66: 1722-1728.
- Ridgway MS, Shuter BJ, 1994. The effects of supplemental food on reproduction in parental male smallmouth bass. *Environ Biol Fishes* 39:201-207.
- Rogers JB, Burley CC, 1991. A sigmoid model to predict gastric evacuation rates of smallmouth bass (*Micropterus dolomieu*) fed juvenile salmon. *Can J Fish Aquat Sci* 48:933-937.
- Sabat AN, 1994. Cost and benefits of parental effort in a brood-guarding fish (*Ambloplites rupestris*, Centrarchidae). *Behav Ecol* 5: 195-201.
- Sargent RC, 1988. Parental care and egg survival both increase with clutch size in the fathead minnow, *Pimephales promelas*. *Behav Ecol Sociobiol* 23:33-37.
- Skolbekken R, Utne-Palm AC, 2001. Parental investment of male two-spotted goby, *Gobiusculus flavescens* (Fabricius). *J Exp Mar Biol Ecol* 261:137-157.
- Smith C, Wootton RJ, 1994. The cost of parental care in *Haplochromis 'argens'*. *Environ Biol Fishes* 40:99-104.
- Steinhart GB, Marschall EA, Stein RA, 2004. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. *Trans Am Fish Soc* 133:121-131.
- Steinhart GB, Wurtsbaugh WA, 2003. Winter ecology of kokanee (*Oncorhynchus nerka*): implications for salmon management. *Trans Am Fish Soc* 132:1076-1088.
- Suski CD, Phelan FJS, Kubacki MF, Philipp DP, 2002. The use of sanctuaries for protecting nesting black bass from angling. In: *Black bass: ecology, conservation, and management*. American Fisheries Society, Symposium 31 (Philipp DP, Ridgway MS, eds). Bethesda, Maryland; 371-378.
- Suski CD, Svec JH, Ludden JB, Phelan FJS, Philipp DP, 2003. The effect of catch-and-release angling on the parental care behavior of male smallmouth bass. *Trans Am Fish Soc* 132:210-218.
- Sutton SG, Bult TP, Haedrich RL, 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon. *Trans Am Fish Soc* 129:527-538.
- Tolonen P, Korpimäki E, 1996. Do kestrels adjust their parental effort to current or future benefit in a temporally varying environment? *Ecoscience* 3:165-172.
- Townshend TJ, Wootton RJ, 1985. Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behavior of the convict cichlid, *Cichlasoma nigrofasciatum*. *Anim Behav* 33:494-501.
- Trautman MB, 1981. *The fishes of Ohio*. Columbus, Ohio: The Ohio State University Press.
- Whitledge GW, Hayward RS, Zweifel RD, Rabeni CF, 2003. Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. *Trans Am Fish Soc* 132:316-325.
- Wiehn J, Korpimäki E, 1997. Food limitation on brood size: experimental evidence in the Eurasian kestrel. *Ecology* 78:2043-2050.
- Williams GC, 1966. Natural selection, costs of reproduction, and a refinement of Lack's principle. *Am Nat* 687-690.
- Willson MF, Morrison JL, Sieving KE, De Santo TL, Santisteban L, Díaz I, 2001. Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conserv Biol* 15:447-456.