

# Condition-dependent nesting in bluegill sunfish *Lepomis macrochirus*

LUCA M. CARGNELLI and BRYAN D. NEFF\*

Restoration Programs Division, Environment Canada, 867 Lakeshore Road, Burlington, Ontario L7R 4A6, Canada; and \*Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada

## Summary

1. There are two prominent, nonmutually exclusive hypotheses to explain the timing of reproduction in animals: energetic constraint and adaptive behaviour.
2. We tested these hypotheses by quantifying the costs and benefits of nesting at different times in the season for male bluegill sunfish *Lepomis macrochirus*, a species with paternal care, in Lake Opinicon (Ontario, Canada).
3. The value of nesting at different times during the breeding season ( $RS_b$ ) was determined from spawning individuals as  $RS_b = P_b \times C_b \times S_b \times O_b$ , where  $P_b$  is the probability of spawning during each bout  $b$ ,  $C_b$  is the expected brood size,  $S_b$  is the expected brood survivorship to 'swim-up', and  $O_b$  is the survivorship of free-swimming fry to age 1 year.
4. The results show that the value of nesting peaks during the middle of the season. However, nesting patterns varied with male condition and not all males nested at the peak.
5. Larger males, which were able to nest multiple times, first nested early in the season when overwinter survivorship of offspring and renesting opportunities later in the season were maximized. These males had the highest seasonal reproductive success.
6. Smaller males, which nested a single time, delayed nesting until the middle of the season when spawning opportunities and brood sizes were greatest.
7. These data suggest that both energetics and adaptive behaviour play roles in determining the timing of reproduction.

*Key-words:* behaviour, Centrarchidae, nesting strategies, reproductive success, sunfish.

*Journal of Animal Ecology* (2006) **75**, 627–633

doi: 10.1111/j.1365-2656.2006.01083.x

## Introduction

In many animals, breeding occurs over a protracted reproductive season with individuals making decisions about when to breed. These decisions often result in individuals of different phenotypes (e.g. age, size, condition) breeding at different times in the season. Often it is larger, older or better condition individuals that breed early in the season, while smaller, younger or lower condition individuals breed later in the season (Lack 1954). Examples of such patterns of reproduction have been reported in many vertebrates, including birds (e.g. Perrins 1966; Price, Kirkpatrick & Arnold 1988), fish (e.g. Ridgway, Shuter & Post 1991; Danylchuk & Fox 1994) and mammals (e.g. Fairbairn 1977; McAdam & Millar 1999).

Most research on the timing of reproduction has emphasized the constraining influence of energy reserves.

For example, in smallmouth bass *Micropterus dolomieu*, Ridgway *et al.* (1991) found that larger males nested earlier in the season and proposed that energetic constraints prevented smaller individuals from breeding early. The authors proposed that larger males should emerge from the winter starvation period in better energetic condition than smaller males because larger fish have lower metabolic rates (Brett & Groves 1979; Schultz & Conover 1999; also see Wiegmann *et al.* 2004), and with less of an energy deficit to make up, larger males should be ready to nest earlier than smaller males. The pattern of older (larger) individuals spawning earlier in the season than younger individuals is well supported in marine teleosts (e.g. Lambert 1987; Berkeley, Chapman & Sogard 2004a; Berkeley *et al.* 2004b). Older individuals may also spawn for a longer period of time as has been shown, for example, in the Atlantic cod *Gadus morhua* (Trippel 1998). Older individuals also can produce higher quality offspring that are more likely to survive to reproduction than smaller individuals, independent of when they are born (Birkeland & Dayton 2005). For example, in the black

rockfish *Sebastes melanops*, older females provide their larvae with more triacylglycerol lipids, which leads to faster larval growth and greater resistance to starvation (Berkeley *et al.* 2004a,b).

Individuals within a population also may breed at different times of the season to maximize their fitness. For example, Schultz, Clifton & Warner (1991) interpreted late season breeding by California surfperch *Micrometrus minimus* as an adaptive tactic utilized by individuals to maximize their fitness. They found that small females delayed breeding independent of their lipid reserves and these females realized greater proportional increases in fecundity due to delayed breeding than large females. The authors concluded that for small females the increases in fecundity outweigh the reduction in offspring survivorship and thus these females delayed breeding to maximize their reproductive success. In another study on sticklebacks *Gasterosteus aculeatus*, Candolin & Voigt (2003) found that early arrival to breeding areas is costly due to higher predation rates, but small males actually arrived earlier to breeding areas than large males. They showed that arrival time did not affect a large male's ability to secure a nest site, but it did affect a small male's ability. Early arriving small males were more likely to secure and retain a nesting site than late arriving small males.

In this study, we examine nesting behaviour in the bluegill sunfish *Lepomis macrochirus* (Rafinesque). It has previously been demonstrated that offspring from early season bluegill nests have higher survivorship to age 1 year (Cargnelli & Gross 1996) and that larger males emerge from winter in better energetic condition than smaller males (Cargnelli & Gross 1997). Here, we use data from naturally spawning individuals to estimate the value of nesting at different times in the breeding season as well as the overall reproductive success associated with different seasonal nesting strategies (i.e. nesting once, twice, or three times). Although we did not manipulate male spawning behaviour, our study suggests that there is no single best time to nest for all males, that phenotypic condition influences when and how many times a male nests, and that, contrary to evidence from birds, the early part of the season is not the best time to nest. Thus, these data indicate that both energetic constraints and adaptive behaviour govern nesting patterns in bluegill. We discuss the implications of our results for the management of fish populations.

## Methods

### BLUEGILL REPRODUCTIVE BIOLOGY

The bluegill (Centrarchidae) is found in eastern and central North America (Scott & Crossman 1973). Our study site is on Lake Opinicon (44°34'N, 76°19'W), which is an 890 ha, mesotrophic lake in Ontario, Canada. In Lake Opinicon, bluegill breed during May to July in distinct periods called bouts, which consist of a group

of colonies that form and spawn within several days of each other. Spawning is initiated by males who enter the littoral zone, construct a nest in the substrate, and actively defend their nest from other males. Nests are built side-by-side in colonies that vary in size from a few nests to 300 nests and the nests serve to raise the young to independence. One to several days later, females approach the colonies in schools and individually enter nests to spawn. Spawning can last for several hours to a full day before the females leave the colony area for deeper waters. Parental males remain to care for the eggs and larvae in their nests for between 7 and 10 days (Gross 1982). Parental care consists of fanning eggs and guarding eggs and larvae from brood predators, and it is energetically costly to males (Coleman & Fischer 1991). Males that have not successfully spawned generally abandon their nest following spawning and leave the colony area. A spawning bout is considered complete when parental care ceases at fry swim-up and the parental males leave the colony area.

### NESTING PATTERNS

All bluegill reproductive activity within our study area (a c. 2 km stretch of shoreline) was surveyed daily by swimmers during 1990–93. We collected data comprising the dates when each colony formed, when spawning occurred, when eggs hatched, and when fry left the nest (swim-up). We also recorded the number of nests in each colony at the time of spawning, the number of males that successfully attracted females and spawned, and the number of males that successfully produced free-swimming fry. On the day after spawning, parental males were individually collected and measured for total length, and their brood size was estimated using an established egg scoring method (Claussen 1991; Cargnelli & Gross 1996). The score is based on the percentage of egg coverage in the nest (on a scale of 1–5) and is highly correlated with the actual number of eggs in the nest as well as the number of fry present in the nest on the day prior to swim-up (Claussen 1991):

1. Eggs:  $r_s = 0.96$ ,  $n = 32$ ,  $P < 0.001$ ; 1 (27–4889 eggs), 2 (4666–28 806), 3 (27 072–53 221), 4 (49 369–86 552), 5 (82 063–112 810).
2. Fry:  $r_s = 0.88$ ,  $n = 31$ ,  $P < 0.001$ ; 1 (1729–6616 fry), 2 (3457–11 910), 3 (5029–16 762), 4 (11 001–23 819), 5 (18 072–27 348).

During the collection of the parental male, a wire screen was placed over the nest to prevent predation of the brood. Upon completion of measurements, parental males were returned to their nests where they typically immediately resumed parental care activities.

Although surveys were performed over 4 years, only data from 1993 are presented in the main text because it was the most complete data set and the only data set for which we had estimates of overwinter survivorship of young-of-year; similar results were found in the other years and we present those results in Appendix S1.

## REPRODUCTIVE SUCCESS

The reproductive success (RS) associated with nesting in each of the breeding bouts was calculated as  $RS_b = P_b \times C_b \times S_b \times O_b$ ; where for each bout  $b$ ,  $P_b$  is the probability of spawning,  $C_b$  is the average brood size,  $S_b$  is the probability of successfully rearing the brood to swim-up, and  $O_b$  is the offspring survivorship to age 1 year.  $P_b$  was calculated by dividing the number of males with eggs in their nest by the total number of males that built nests during each bout.  $C_b$  was calculated by summing the egg scores for a bout and then dividing by the number of males that received eggs.  $S_b$  was calculated as the number of males that produced free-swimming fry divided by the number of males that received eggs in each bout.  $O_b$  was calculated by ageing juveniles collected in the spring of 1994 back to the day (and hence bout) they were born and dividing the number of juveniles born in each bout by the number of fry produced (see Cargnelli & Gross 1996). Briefly, 400 age-1 bluegill were captured from within our study area on 24 May 1994 using a seine and minnow traps. The total length (mm) and wet weight (g) of each individual were measured. Otolith daily rings were used to age a random subsample of these individuals ( $n = 161$ ). The otolith daily ring counts were used to back-calculate dates of swim-up and to assign each individual to a spawning bout in 1993. A detailed description of otolith ageing methods is provided in Cargnelli & Gross (1996).

## NESTING TACTICS AND STRATEGIES

From the years 1990–93, a haphazard selection of parental males that nested during each bout were tagged shortly after spawning and their nesting activity was monitored for the duration of the season to determine reneating rates (80 males in 1993 and 714 males in 1990–92). Floy brand T-tags were inserted into the muscle directly below the dorsal fin on the left side of the body. During subsequent bouts, the colony locations of tagged males that reneated were recorded. Rates of reneating were determined for each bout as the proportion of tagged males that reneated later in the season.

For each 'nesting strategy' (i.e. nesting once, twice or three times), we determined all possible combinations of bouts, which we termed 'nesting tactics.' For two-nesting and three-nesting strategies, not all nesting tactics were possible because males provide parental care and take time-off between nesting attempts, presumably to replenish energy reserves (Coleman & Fischer 1991). It is reasonable to assume that the longer a male remains on the nest, the longer the time between nesting attempts. For two- and three-nest strategies, we calculated the average interval between nesting attempts (I) using the equation  $I = PC + OT$ , where PC is the length of the parental care period (i.e. brood development time) and OT is the off-time between nest abandonment and the initiation of the next nest. The mean PC was calculated for each bout as the number of days

between colony spawning and the swim-up of fry from the nest. OT was calculated based on our tagged males that nested two or three times during the season. We used linear regression to determine the relationship between OT ( $y$ -variable) and the length of the previous nesting attempt, PC ( $x$ -variable). We also used a logistic regression to examine the relationship between PC and the probability of reneating. The interval values (I) determined for each bout were used to determine all possible nesting tactics, and the reproductive success data ( $RS_b$ ) was used to calculate the total reproductive success associated with each nesting tactic. This model does assume that I is dependent on breeding time in the season and not male state. A more comprehensive estimate of I would involve manipulation of individuals' energetic state during each breeding bout. However, this was beyond the scope of the current study.

All statistics were performed with SPSS (v. 13.0). Mean values of data are reported plus or minus 1 SE.

## Results

## NESTING PATTERNS

There were eight breeding bouts in 1993 involving a total of 106 colonies and 3059 males. Of these males, 1825 (60%) successfully spawned and 1278 (42%) successfully produced free-swimming fry. The first spawning occurred on 6 June and the final spawning occurred on 13 July. The number of breeding males varied significantly among bouts ( $\chi^2 = 882$ , d.f. = 1,  $P < 0.001$ ), with most males breeding during the middle of the season (Fig. 1a). There was a progressive decline in the body length of nesting parental males through the breeding season (ANOVA:  $F_{7,696} = 10.4$ ,  $P < 0.001$ ; Fig. 1b).

Duration of parental care (i.e. brood development time) was negatively correlated with daily mean water temperature (taken at 1 m depth:  $r_p = -0.89$ ,  $n = 88$ ,  $P < 0.001$ ) and water temperature was positively correlated with spawning date of each colony ( $r_p = 0.97$ ,  $n = 88$ ,  $P < 0.001$ ). Consequently, duration of parental care ranged from an early season high of 10 days to a late-season low of about 5 days (ANOVA:  $F_{7,82} = 45.1$ ,  $P < 0.001$ ).

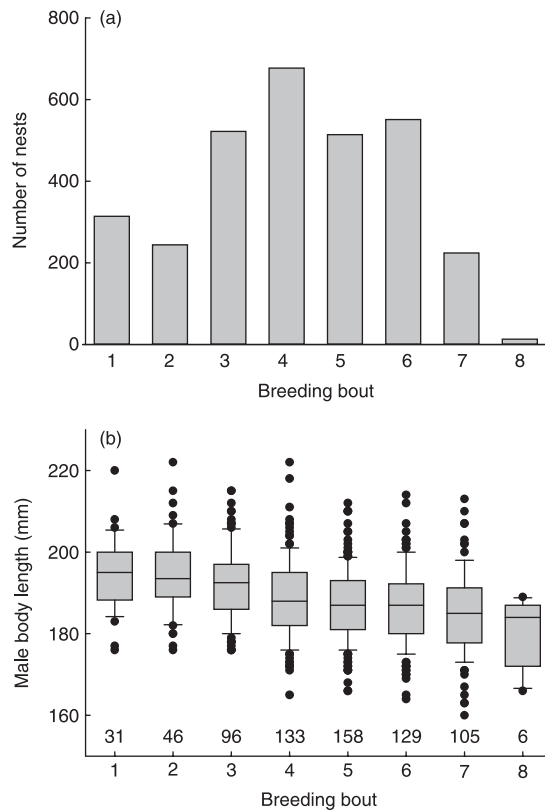
## REPRODUCTIVE SUCCESS

The probability that a nesting male successfully spawned,  $P_b$ , varied significantly across the breeding season ( $\chi^2 = 274$ , d.f. = 1,  $P < 0.001$ ), typically increasing with each successive bout (Table 1, Fig. 2a). Mean brood size,  $C_b$ , also varied significantly across the breeding season ( $\chi^2 = 18.9$ , d.f. = 1,  $P < 0.001$ ), peaking during the middle of the season (Table 1, Fig. 2b). The probability that a brood was successfully reared to fry swim-up,  $S_b$ , increased during each successive bout until the final bout ( $\chi^2 = 52.6$ , d.f. = 1,  $P < 0.001$ ; Table 1, Fig. 2c). Survivorship to age 1 year was markedly greater for offspring born in the first bout as compared with the other bouts (Table 1, Fig. 2d), likely because offspring

**Table 1.** The value of nesting in each spawning bout during the 1993 breeding season for bluegill sunfish *Lepomis macrochirus* in Lake Opinicon, Ontario.  $P_b$  is the probability of spawning,  $C_b$  is the expected brood size,  $S_b$  is the expected brood survival,  $O_b$  is the expected offspring survival to age 1 year and  $RS_b$  is the standardized reproductive success from each bout

Bout	$P_b$	$C_b$	$S_b$	$O_b$	$RS_b$
1	0.019 (6/314)	1.333 (4/3)	0.333 (2/6)	79.8	1.21
2	0.324 (79/244)	1.759 (139/79)	0.354 (28/79)	4.69	1.69
3	0.592 (309/522)	1.890 (533/282)	0.521 (161/309)	1.50	1.56
4	0.687 (465/677)	2.176 (668/307)	0.662 (308/465)	0.56	1.00
5	0.660 (339/514)	1.981 (515/260)	0.743 (252/339)	1.09	1.90
6	0.768 (423/551)	1.943 (544/280)	0.837 (354/423)	0.64	1.42
7	0.853 (191/224)	1.701 (279/164)	0.874 (167/191)	0.64	1.44
8	1.000 (13/13)	1.462 (19/13)	0.462 (6/13)	1.23	1.48

Numbers in parentheses indicate samples sizes. For example, for  $P_1$ , six of 314 nesting males were successful at spawning, for  $C_1$ , a total egg score of 4 was obtained by three successful males for which we had egg score data (we did not have egg score data for all males), and for  $S_1$ , two of the six males that spawned were successful at producing free-swimming fry.



**Fig. 1.** Nesting patterns across the eight breeding bouts in 1993 for bluegill sunfish *Lepomis macrochirus* in Lake Opinicon, Ontario. (a) The distribution of nesting males in each bout and (b) box plots of body length of nesting males in each bout. Boxes denote 25th, 50th and 75th percentiles, whiskers denote 10th and 90th percentile and filled circles denote males outside of the 10–90 percentile. Numbers below the box plots are sample sizes.

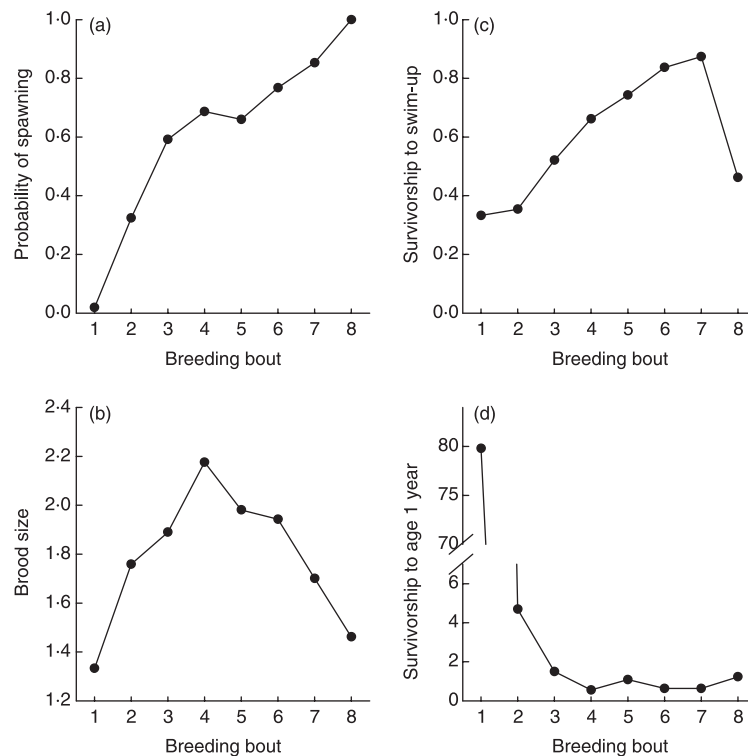
born in the first bout have a longer growing season before entering the winter starvation period (Cargnelli & Gross 1996).

Table 1 summarizes the expected reproductive success,  $RS_b$ , for each breeding bout. Bout 5 had the highest reproductive success, which was 12% higher than the second best bout (bout 2) and 90% higher than the worst bout (bout 4).

#### NESTING TACTICS AND STRATEGIES

Overall, only 16% of males nested multiple times (based on the 794 males tagged during 1990–93). However, among males that nested for the first time during the first or second breeding bout, 53% nested multiple times with 83% of these males nesting twice and 17% nesting three times. Of these males, those that nested multiple times were larger than those that nested only a single time (multiple nests:  $197 \pm 2$  mm; single nest:  $192 \pm 1$  mm;  $t_{72.8} = 2.22$ ,  $P = 0.03$ ). Examining the OT for the interval between first and second nesting attempts and the length of the first nesting attempt (PC), the regression slope was not significantly different from 0 ( $R^2 = 0.08$ ,  $\beta = -0.28$ ,  $n = 41$ ,  $P = 0.074$ ). This result indicates that the OT between first and second nests was close to constant and could be assumed to be  $OT_{1-2} = 5$  days. There also was no relationship between PC and the probability of renesting ( $\chi^2 = 0.29$ , d.f. = 1,  $P = 0.59$ ). Conversely, for the interval between second and third nesting attempts there was a strong positive relationship between OT and PC ( $R^2 = 0.68$ ,  $\beta = 0.82$ ,  $n = 7$ ,  $P = 0.023$ ); the longer the duration of the second nest, the longer the OT prior to nesting a third time. From the regression equation we determined that  $OT_{2-3} = 0.61 + 0.88 \times PC$  days. There also was a trend between PC and the probability of renesting ( $\chi^2 = 3.37$ , d.f. = 1,  $P = 0.066$ ); males that provided more care were less likely to renest. Based on these relationships, we determined that 15 of the 28 nesting tactics were energetically possible within the two-nest strategy, while only two of the 112 nesting tactics were possible within the three-nest strategy (Table 2).

Based on the reproductive success data for each bout (see Table 1), an individual that nested only once would do best to nest during bout 5, when the value of a single brood is maximized. An individual nesting twice would do best by nesting during bouts 2 and 5 and an individual nesting three times would do best nesting during bouts 1, 4 and 8. Although the three-nest strategy yielded higher seasonal reproductive success than the two- or one-nest strategies, neither three-nest tactic included the single best time to nest (bout 5).



**Fig. 2.** Reproductive success associated with the eight breeding bouts in 1993 for bluegill sunfish *Lepomis macrochirus* in Lake Opinicon, Ontario. The panels display the: (a) probability of spawning,  $P_b$ ; (b) average brood size,  $C_b$ ; (c) brood survivorship to swim-up,  $S_b$ ; and (d) relative survivorship of free-swimming fry to age 1 year,  $O_b$ . Sample sizes for each data point are presented in Table 1.

**Table 2.** The reproductive success (RS) associated with combinations of nesting tactics within each of the three nesting strategies for bluegill sunfish *Lepomis macrochirus* breeding in Lake Opinicon, Ontario. Only the tactics which are possible based on estimated time constraints are listed. The number of renesting males (No) performing each tactic are also shown

Bout	One nest		Two nests			Three nests		
	RS	No	Bouts	RS	No	Bouts	RS	No
5	1.90	4	2 and 5	3.59	4	1, 4 and 8	3.69	1
2	1.69	—	5 and 8	3.38	—	1, 4 and 7	3.67	2
3	1.56	—	2 and 8	3.17	—			
8	1.48	—	2 and 7	3.13	—			
7	1.44	—	2 and 6	3.11	—			
6	1.42	3	1 and 5	3.11	3			
1	1.21	—	3 and 8	3.04	—			
4	1.00	—	3 and 7	3.00	—			
		1	3 and 6	2.98	1			
		—	1 and 8	2.69	—			
		—	1 and 7	2.65	—			
		1	1 and 6	2.63	1			
		—	4 and 8	2.48	—			
		—	4 and 7	2.44	—			
		16	1 and 4	2.21	16			

Reproductive success data are based on those shown in Table 1 and renesting data are based on tagged males from 1993.

## Discussion

Our results show that the number of nesting bluegill varies considerably through the breeding season, with the

majority of males nesting during the middle of the season and the largest males nesting during the early part of the season. These data would appear to be consistent with the energetic constraint hypothesis. However, in this study we determined the reproductive success associated with each breeding bout and found that it was not greatest early in the season despite the high offspring survivorship to age 1 year. Instead, reproductive success was highest during the middle of the breeding season. Thus, energetics alone cannot explain nesting patterns for male bluegill.

Why then do large, high-condition bluegill males nest early in the season if they could instead obtain higher reproductive success by nesting later in the breeding season? For males that can nest multiple times, the challenge may not be to nest in the single bout that maximizes reproductive success but to optimally allocate reproductive effort across the entire breeding season. Indeed, we determined that the three-nest strategy did not actually include the single best time to breed (see Table 2). This result is in agreement with breeding patterns in birds, which shows that individuals that nest multiple times during the breeding season are pulled off the single optimal nesting time (Rowe, Ludwig & Schluter 1994). For bluegill, the only way for a male to produce three successful broods in a single season is to start during the first bout of spawning and this explains why the largest, highest quality males nest early in the season (Cargnelli & Gross 1997). Conversely, males that nest only a single time maximize their reproductive success by nesting during the middle of the season.

Energetic constraints appear to influence the amount of investment into reproduction that an individual is able to make (nesting strategy), while adaptive decision-making influences how this energy is allocated (nesting tactic). Our results therefore provide support for both the energetic constraint hypothesis and the adaptive behaviour hypothesis, and add to a growing body of empirical research showing that energetics as well as other trade-offs govern nesting patterns (e.g. Schultz *et al.* 1991; Candolin & Voigt 2003; Dickerson *et al.* 2005).

How do the predictions of our model fit with the results of our tagging study? First, the males that produced three successful broods nested according to the two possible tactics predicted by the model (see Table 2). Second, of the males that nested twice, several used the tactic predicted to be the most successful. However, the most frequent two-nest tactic that we observed was ranked as the worst tactic of the two-nest strategy (bouts 1 and 4). It is possible that these males were planning to nest a third time but were unable to due to energetic constraints, or that they did in fact nest a third time but re-nested outside of our study area. It is also possible that an unsuccessful spawning attempt will alter a male's optimal nesting tactic. For example, a male who nested for the first time in bout 2 but was unsuccessful at obtaining eggs and abandoned the nest might re-nest again at the earliest opportunity (i.e. bout 3). It is also possible that the costs and benefits of nesting at different times during the season are state-dependent (e.g. condition or size). Because our model is based on the averages for only males that actually attempted to nest during each bout, we cannot rule out that the value of breeding in each bout differs for males that did not attempt to nest from those we measured (see Schultz *et al.* 1991). Our model also may underestimate the value of breeding early because it does not incorporate the increased future breeding potential of early born offspring that might result from their increased size. Furthermore, the survivorship estimates to age 1 year associated with each bout may vary from year to year due to, for example, variation in climate (see Garvey, Herra & Leggett 2002 for estimates from 1998; also see Santucci & Wahl 2003). Finally, males should behave in a way that maximizes their lifetime reproductive success rather than their seasonal reproductive success. Males may trade-off present reproductive success for higher winter survival to the next breeding season. Thus, the tactic that maximizes lifetime reproductive success may not necessarily be the best single season tactic. Our analysis was unable to incorporate interseasonal breeding patterns in part because the tags typically fall out during the winter.

Selective pressures leading to the nesting patterns observed in bluegill may differ from those leading to the nesting patterns observed in other species. In some bird species, early nesters have the greatest seasonal reproductive success, stemming from the fact that both clutch size and offspring survival are greatest early in the season (Price *et al.* 1988; Rowe *et al.* 1994). Thus, there is direct selection in these species for early nesting

(also see Perrins 1966; Westneat 1992). Conversely, in bluegill, there is no direct selection for early nesting; the first bout is one of the worst times to breed with respect to reproductive success. Bluegill males nesting in the first bout are instead trying to maximize the number of nesting attempts during the breeding season and thereby maximize their seasonal reproductive success. Thus, in bluegill, direct selection is on multiple nesting, which as a consequence leads to selection for early nesting.

The results of our study may have important implications for management of fish species with similar multi-bout spawning seasons. The early part of the bluegill reproductive season is when the largest, highest-condition individuals are spawning and it is when the most valuable fry are produced in terms of year 1 body size and overwinter survivorship. This is contrary to management strategies that protect peak spawning times, for example through closure of fishing seasons, because the strategies assume peak spawning times are the most important to recruitment. Our data show that early, nonpeak spawning times should be protected. Analogous recommendations have been made in other fish, including the groundfish, where, for example, it has been demonstrated that older female black rockfish provide larvae with more triacylglycerol lipids that leads to greater resistance to starvation and higher growth (Berkeley *et al.* 2004a,b).

Finally, little is known about the role that bluegill females play in the patterns observed in the current study. Although in another study we found no relationship between female body length or condition and timing of breeding (unpublished data), further study is warranted.

### Acknowledgements

We thank Don Jackson, Joe Repka, Mark Ridgway, Locke Rowe, two anonymous reviewers and especially Mart Gross for helpful discussion and comments on the manuscript. Louise Porto provided field assistance at the Queen's University Biological Station. This research was conducted during the authors' graduate studies in the lab of Mart Gross at the University of Toronto. The research was funded by the NSERC of Canada and conformed to animal care protocols outlined by the Canadian Council on Animal Care.

### References

- Berkeley, S.A., Chapman, C. & Sogard, S.M. (2004a) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**, 1258–1264.
- Berkeley, S.A., Hixon, M.A., Larson, R.J. & Love, M.S. (2004b) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, **29**, 23–32.
- Birkeland, C. & Dayton, P.K. (2005) The importance in fishery management of leaving the big ones. *Trends in Ecology and Evolution*, **20**, 356–358.
- Brett, J.R. & Groves, T.D.D. (1979) Physiological energetics. *Fish Physiology*, Vol. VIII (eds W.S. Hoar, D.J. Randall & J.R. Brett), pp. 279–352. Academic Press, New York.

- Candolin, U. & Voigt, H.-R. (2003) Size-dependent selection on arrival times in sticklebacks: why small males arrive first. *Evolution*, **57**, 862–871.
- Cargnelli, L.M. & Gross, M.R. (1996) The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 360–367.
- Cargnelli, L.M. & Gross, M.R. (1997) Fish energetics: larger individuals emerge from winter in better condition. *Transactions of the American Fisheries Society*, **126**, 153–156.
- Claussen, J.E. (1991) Annual variation in the reproductive activity of a bluegill population: effect of clutch size and temperature. MSc Thesis, University of Toronto, Ontario, Canada.
- Coleman, R.M. & Fischer, R.U. (1991) Brood size, male fanning effort and the energetics of a non-shareable parental investment in bluegill sunfish, *Lepomis macrochirus* (Teleostei: Centrarchidae). *Ethology*, **87**, 177–188.
- Danylchuk, A.J. & Fox, M.G. (1994) Age and size-dependent variation in the seasonal timing and probability of reproduction among mature female pumpkinseed, *Lepomis gibbosus*. *Environmental Biology of Fishes*, **39**, 119–127.
- Dickerson, B.R., Brinck, K.W., Willson, M.F., Bentzen, P. & Quinn, T.P. (2005) Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology*, **86**, 347–352.
- Fairbairn, D.J. (1977) Why breed early? A study of reproductive tactics in *Peromyscus*. *Canadian Journal of Zoology*, **55**, 862–871.
- Garvey, J.E., Herra, T.P. & Leggett, W.C. (2002) Protracted reproduction in sunfish: the temporal dimension in fish recruitment revisited. *Ecological Applications*, **12**, 194–205.
- Gross, M.R. (1982) Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. *Zeitschrift für Tierpsychologie*, **60**, 1–26.
- Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Oxford University Press, Oxford.
- Lambert, T.C. (1987) Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the population. *Marine Ecology Progress Series*, **39**, 209–220.
- McAdam, A.G. & Millar, J.S. (1999) Breeding by young-of-the-year female deer mice: Why weight? *Ecoscience*, **6**, 400–405.
- Perrins, C.M. (1966) Survival of young manx shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. *Ibis*, **108**, 132–135.
- Price, T., Kirkpatrick, M. & Arnold, S.J. (1988) Directional selection and the evolution of breeding date in birds. *Science*, **240**, 798–799.
- Ridgway, M.S., Shuter, B.J. & Post, E.E. (1991) The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *Journal of Animal Ecology*, **60**, 665–681.
- Rowe, L., Ludwig, D. & Schluter, D. (1994) Time, condition, and the seasonal decline of avian clutch size. *American Naturalist*, **143**, 698–722.
- Santucci, V.J. & Wahl, D.H. (2003) The effects of growth, predation, and first-winter mortality on recruitment of bluegill cohorts. *Transactions of the American Fisheries Society*, **132**, 346–360.
- Schultz, E.T. & Conover, D.O. (1999) The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. *Oecologia*, **119**, 474–483.
- Schultz, E.T., Clifton, L.M. & Warner, R.R. (1991) Energetic constraints and size-based tactics: the adaptive significance of breeding-schedule variation in a marine fish (Embiotocidae: *Mictometrus minimus*). *American Naturalist*, **138**, 1408–1430.
- Scott, W.B. & Crossman, E.J. (1973) Freshwater fishes of Canada. *Bulletin of the Fisheries Research Board of Canada*, **184**, 1–966.
- Trippel, E.A. (1998) Egg size and viability and seasonal offspring production of young Atlantic cod. *Transactions of the American Fisheries Society*, **127**, 339–359.
- Westneat, D.F. (1992) Nesting synchrony by female red-winged blackbirds: effects of predation and breeding success. *Ecology*, **73**, 2284–2294.
- Wiegmann, D.D., Angeloni, L.M., Baylis, J.R. & Newman, S.P. (2004) Negative maternal or paternal effects on tactic inheritance under a conditional strategy. *Evolution*, **58**, 1530–1535.

Received 25 August 2005; accepted 4 January 2006

### Supplementary material

The following supplementary material is available for this article online.

**Appendix S1.** Comparison of bluegill sunfish *Lepomis macrochirus* reproductive data collected from the fish reproduction study area at Lake Opinicon, Ontario from 1990 through 1993