Behav Ecol Sociobiol (2004) 56:381–387
DOI 10.1007/s00265-004-0792-7

ORIGINAL ARTICLE

Bryan D. Neff · Luca M. Cargnelli · Isabelle M. Côté

Solitary nesting as an alternative breeding tactic in colonial nesting bluegill sunfish (*Lepomis macrochirus*)

Received: 10 November 2003 / Revised: 1 March 2004 / Accepted: 18 March 2004 / Published online: 22 April 2004

Abstract Colonial breeding can evolve in response to benefits afforded by clumped individuals, such as reduced predation and increased ease of assessing potential mates. However, colonial breeding can also impose costs such as increased disease transmission or increased cuckoldry. Here, we investigate solitary nesting as a potential alternative breeding tactic in colonial breeding bluegill sunfish (*Lepomis macrochirus*). Most male bluegill, termed parentals, compete for nesting sites in colonies and then court and spawn with females and provide sole care of the eggs. Although nesting in a colony results in reduced predation and fungal infection of broods, it comes at a cost of increased parasitism by specialized cuckolder males that do not nest. We found that 4.5% of parentals forgo spawning in a colony and instead construct nests solitarily. Solitary males were of similar size and age to colonial males, but were in significantly better condition. Solitary males obtained as many eggs as males nesting in the center of colonies, and significantly more than males nesting on the periphery of colonies. Thus, females do not appear to discriminate against solitary males. Solitary males had smaller ear tabs, a presumed sexually selected character used by parental males in intrasexual competition, than colonial males. Tracking data revealed consistency in nesting tactic (but not nest position within the colony) between spawning attempts. We suggest that solitary nesting represents either a facultative decision made by parental males in top condition at the onset of breeding, or a life history decision to forgo spawning in colonies.

Keywords Coloniality · Mating systems · Tactic · Female choice · Bluegill

Communicated by K. Lindström

B. D. Neff (✉)
Department of Biology,
University of Western Ontario,
London, ON, N6A 5B7, Canada
e-mail: bneff@uwo.ca
Tel.: +1-519-8502532
Fax: +1-519-6613935

L. M. Cargnelli
Ontario Ministry of Natural Resources,
Lake Erie Management Unit,
London, ON, N6E 1L3, Canada

I. M. Côté
Centre for Ecology, Evolution and Conservation,
School of Biological Sciences,
University of East Anglia,
Norwich, NR4 7TJ, UK

Introduction

Social behavior is usually defined by interactions between conspecifics (Wilson 1975). One common form of social behavior is colonial breeding, where individuals congregate on densely distributed territories that contain no resources other than nest sites. The evolution of coloniality has attracted the attention of behavioral ecologists for decades. Coloniality is widespread in the animal kingdom (Höglund and Alatalo 1995; Danchin and Wagner 1997) and is commonly studied by examining the costs and benefits to group nesting. Sexual selection underlies many of the hypotheses that have gained support (Parker 1978; Tyler 1995; Danchin and Wagner 1997; but see Brown and Brown 2000; Møller 2002).

Colonial breeding is found in many fish and typically appears to have evolved in response to anti-predation benefits. In the coral reef fish *Abudefduf abdominalis*, for example, colonial nesting reduces egg predation and females prefer to mate with males in larger colonies (Tyler 1995). In the sand tilefish *Malacanthus plumieri*, colonial individuals also benefit from reduced predation but experience increased intrasexual aggression (Baird and Baird 1992).

Colonial breeding has also been studied extensively in the bluegill sunfish (*Lepomis macrochirus*). Bluegill colonies are clearly social aggregations because there are abundant, yet unused nesting sites of equivalent quality available (Gross and MacMillan 1981). Although most males nest in colonies, a small proportion of males nest solitarily. Gross and MacMillan (1981) found that colonial nesting bluegill benefit from group mobbing of brood predators and predator swamping effects (see also Dominey 1981, 1983). Particularly, nests located in the center of a colony receive the most protection from group mobbing. Côté and Gross (1993) also found that fungal infection by *Saprolegnia* sp. is lower in colonies than in solitary nests, possibly because of the increased time males can spend caring for the eggs (due to the sharing of defence) and because of spore dilution effects. However, coloniality also comes at a cost of increased cuckoldry. Cuckoldry rates appear to be considerably higher in colonial nests than solitary nests. Colonial nesting males may fertilize as few as a quarter of the young within their nest, while solitary males appear to be rarely cuckolded (Gross 1991; Neff 2001; see also Keenleyside 1972; Jennings and Philipp 1992). However, it is not yet known if solitary males differ in quality from colonial males, or if females discriminate against solitary males during mating.

Bluegill are native to lakes and rivers of North America, but are now found throughout the world (Lee et al. 1980). Males are characterized by a discrete polymorphism in life histories that have been termed “parental” and “cuckolder” (Gross and Charnov 1980; Gross 1982; see also Dominey 1980). In Lake Opinicon (Ontario, Canada), parentals mature at age 7 years and most compete to construct nests in densely packed colonies, with up to 300 nests built rim-to-rim (Cargnelli 1995). Parentals are aggressive towards conspecifics that attempt to nest near them (Colgan et al. 1979; Gross 1982), and aggressive displays include flaring of the opercular flaps to reveal black “ear tabs”. The latter are prominent extensions on the flaps, which are believed to be an intrasexually selected character (Gross 1982; Côté 1993). Nesting parentals then court and spawn with females, and provide sole parental care for the developing eggs and fry (newly hatched eggs) in their nest for up to 10 days (Gross 1982). Parental care consists of fanning eggs and guarding eggs and fry from brood predators. During the care period parentals do not forage and can lose up to 20% of their body weight (average =11%; Coleman and Fischer 1991). By contrast, cuckolders do not build nests of their own or care for their offspring. Cuckolders mature precociously and steal fertilizations in the nests of parentals using two tactics: “sneakers” (age 2–3 years) hide behind plants and debris near the nest edge, but are visible after darting into the nest during female egg releases; “satellites” (age 4–5 years) are about the size of mature females (age 4–8 years) and by expressing female color and behavior appear to mislead parentals into identifying them as a second female in the nest (Dominey 1980; Neff and Gross 2001).

In this paper, we investigated solitary and colonial nesting in bluegill sunfish by collecting morphological data from nesting parentals and assessing the number of eggs that each male obtained as a measure of female mating preference. Colonial parentals were divided into “peripheral” and “central” based on their nest location within the colony because central nests are less susceptible to predation and therefore may be preferred sites. We also tracked individual parentals during the breeding season to determine if there was consistency in nesting tactic between spawning attempts.

Methods

Study site

Bluegill spawning activity was monitored at our study site on Lake Opinicon (44°34′N, 76°19′W) during the May–July breeding season. Lake Opinicon is an 890-hectare, mesotrophic, warm-water lake in Leeds County, Ontario, Canada (Keast 1978). The lake sustains a large natural population of bluegill whose reproductive biology has been studied since the mid-1970s. For this study, bluegill reproductive activity was examined in an area bounding about 2 km of littoral zone along the northern shore of the lake (map in Gross and Nowell 1980). This zone, referred to as the fish reproduction study area (FRSA), includes a wide variety of habitat types characterizing the wide biological and physical diversity in which bluegill are known to breed.

All bluegill reproductive activity within the FRSA was surveyed by swimmers equipped with snorkeling gear and underwater writing tablets on which observations were recorded. Complete surveys were made on a daily basis beginning before the onset of breeding in May and ending after breeding ceased in July. Data were collected for nesting parentals (colonial and solitary) that formed within the FRSA from 1988 to 1993, and 2002. A solitary nest was defined as a nest that was not within 1 m of another nest (measured from adjacent nest edges; Jennings and Phillip 1992). For colonies, following Gross and MacMillan (1981), parentals were further classified as peripheral when their nest was on the outside border of the colony and had at least one edge exposed or central when there was at least one nest separating their nest from the colony edge. Nests were monitored from the date of formation and for the duration of the parental care period.

Measurements

The day after spawning the number of parentals in the colony was recorded. The brood size of each male was estimated using egg scores. Egg scores were a rank that ranged from 1 to 5, which were assigned based on size and thickness of cover. Claussen (1991) has shown that these scores correlate with the actual number of eggs in a nest [r_s=0.96, P<0.001, n=32; 1 (27–4,889 eggs), 2 (4,666–28,806), 3 (27,072–53,221), 4 (49,369–86,552), 5 (82,063–112,810)] as well as the number of fry that emerge from the nest at the end of the care period [r_s=0.88, P<0.001, n=31; 1 (1,729–6,616 fry), 2 (3,457–11,910), 3 (5,029–16,762), 4 (11,001–23,819), 5 (18,072–27,348)]. The method has been used in other studies as a measure of reproductive success and female mating preference (Cargnelli and Gross 1996; Neff et al. 2003).

Parentals were then collected one at a time from their nest using dip nets. They were transferred to a nearby boat where measurements were quickly taken. These measurements included total body length (nearest mm), weight (0.1 g), and the area of the right ear tab (mm^2). The area was determined from the product of two orthogonal measurements, one taken parallel to the fish’s lateral line. One scale was also collected from each fish and later analyzed to determine the age in years by examining the annuli (i.e., growth rings; see Cargnelli and Gross 1996). Parentals were then returned to their nest where usually they immediately resumed parental care activity. Although nest takeovers during or after spawning occasionally occur in redbreast sunfish, *L. auritus* (DeWoody et al. 1998), tagging data and genetic analysis of paternity have not revealed such behavior in bluegill (e.g., Gross 1982; Neff 2001; authors’ unpublished data). Thus, the parentals collected the day after spawning were assumed to be the same individuals that were present during spawning.

Egg score data were collected in 1988–1990, 1993 and 2002; length data were collected in all years; weights were collected in all years but 1993; ear tab data were collected in 1991–1993 and 2002; and scale samples were collected in 1988–1990 and 2002. Age could not always be conclusively determined from the scale sample because of obscured patterns caused by, for example, scale regeneration. For years in which weight data were collected, Fulton's condition factor was calculated as weight/length^3. This factor was used as a measure of energy because it correlates with mobile lipids and typically outperforms other methods such as residuals from a linear regression of weight onto length (Cargnelli 1995; Neff and Cargnelli 2004; see also Sutton et al. 2000).

Repeat spawning

To ascertain if repeat spawners showed consistency in their nest position, in the years 1988–1990, 1993 and 2002 a total of 901 parentals were tagged using Floy brand T-tags inserted into the muscle directly below the dorsal fin on the left side of the body. The study site was monitored for the duration of the spawning season and the nest position of repeat spawners was recorded. In most cases in which males spawned a second time in a breeding season they were not remeasured. Thus, while we had repeat measures of nest position, we did not have a second estimate of egg score, male length, condition or ear tab area.

Statistical analysis

Statistics were performed using SPSS (v.10). All means are reported plus or minus one standard error and all *P*-values are from two-tailed tests. We did not directly test weight in any analysis because length and weight are highly correlated and weight (adjusted for length) is captured in Fulton's condition factor. We first used Spearman's correlation to investigate the relationship between colony size and the means for egg score, parental male length, condition, ear tab area and age. Only colonies from which we had measured at least four parentals were considered.

We used MANOVA to simultaneously compare the body length, condition and ear tab area of central, peripheral and solitary parentals. We did not include male age in this analysis because we had few individuals for which both ear tab area and age were measured (n=13). Thus inclusion of both variables would significantly reduce the statistical power of the analysis. We chose to omit age because it is highly correlated with body length, which was included in the analysis, and because it is a rank measure. We then used individual ANOVAs and Tukey post hoc to confirm any significant relationship from the MANOVA on the full data set for each measurement. We also used ANOVA to investigate the effects of year, nesting tactic, and the interaction on body condition.

Next, we used a Kruskal-Wallis test to determine if there was a difference in the age or the number of eggs obtained by solitary, central and peripheral males. Mann-Whitney *U*-tests were then used for pair-wise comparisons and the significance levels were adjusted for multiple comparisons. We also used Spearman's correlation to investigate relationships between egg scores and parental length, age, condition and ear tab area. Non-parametric tests were used for the age and egg score data because these variables were categorical.

To investigate the allometric relationship between ear tab area and body length, we used linear regression analysis of logarithm transformed values. The slope of the regression line represents the power relationship between the two variables. Isometric growth indicates that ear tab area should scale to the square of body length (i.e., power =2). The regression analysis was performed separately for central, peripheral and solitary males, and *t*-test was used to investigate differences in the slopes of the regression lines (Zar 1999).

Finally, a two-by-two chi square analysis was used to investigate the consistency of renesting behavior (colonial versus solitary).

Results

A total of 1,014 parentals were collected and measured. These parentals comprised 968 colonial males (433 central and 535 peripheral) from 77 colonies and 46 solitary males. Thus, solitary nesters represented about 4.5% (=46/1,014) of all nesting parentals. Colonies ranged in size from 4 to 272 nests and averaged 55±6 nests. There were no significant relationships between the number of parentals in a colony and the mean egg score, or mean condition, ear tab area or age (Table 1). There may have been a trend for larger colonies to contain males of greater length (P=0.055), but correction for multiple comparisons indicates that this relationship is not significant (corrected alpha level =0.05/5=0.01).

The MANOVA revealed significant differences among central, peripheral and solitary males (overall model: Wilk's lambda =0.82, $F_{6,438}$=7.7, P<0.001) in condition ($F_{2,221}$=17.3, P<0.001) and ear tab area ($F_{2,221}$=5.6, P=0.004), but not body length ($F_{2,221}$=1.4, P=0.253). The individual ANOVAs on the full data sets were analogous to the results from the MANOVA (Table 2). The Tukey post hoc tests showed that solitary males were in significantly better condition but had smaller ear tabs than either central or peripheral males (Fig. 1). There was no difference in the age of the males, but there were differences in the number of eggs each male type obtained (Table 2). Further analysis of the egg score data revealed that there was no difference between central and solitary males (Mann-Whitney: U=7779, P=0.49, n=406), but both were greater than peripheral males (central: U=66214, P<0.001, n=807; solitary: U=7341, P=0.001, n=493; Fig. 2). The significance of these three comparisons does not change when adjusted for multiple comparisons (corrected alpha =0.05/3=0.017). Within each male type, there was no correlation between egg score and male length, age, condition or ear tab area (Spearman's: P>0.07 for each).

The analysis of the effects of year and nesting tactic on condition revealed that both had significant effects (overall: $F_{10,909}$=18.4, P<0.001; tactic: $F_{1,909}$=7.6, P= 0.006; year: $F_{5,909}$=8.8, P<0.001). The interaction term was not significant (tactic × year: $F_{4,909}$=2.2, P=0.071).

Regression analysis showed that there was a significant relationship between body length and ear tab area (logarithm transformed) for central males (r^2=0.14, P<0.001, n=148) and peripheral males (r^2=0.21, P<0.001,

Table 1 Summary of the relationships between colony size (number of nests) and the means of five measurements taken from each colony. The data comprise Spearman's correlation coefficient (r_s), number of colonies (n) and significance value (P)

Measurement	r_s	n	P
Egg score	0.065	37	0.704
Male length	0.260	55	0.055
Male condition	−0.123	48	0.403
Male ear tab area	0.025	29	0.897
Male age	−0.085	25	0.687

Table 2 Summary of the ANOVA and Kruskal-Wallis analyses of five measurements of central, peripheral and solitary males. Measurements are reported as means with one standard error in parentheses

Measurement	Central	Peripheral	Solitary	Statistic[a]	*df*[b]	*P*
Male length (mm)	187.9 (0.5)	187.5 (0.4)	189.8 (1.4)	1.3	2,1011	0.276
Male condition (g/mm^3)	1.73 (0.01)	1.74 (0.01)	1.94 (0.05)	27.4	2,917	<0.001
Male ear tab area (mm^2)	123 (3)	126 (3)	104 (4)	4.2	2,315	0.015
Male age (year)	7.93 (0.07)	8.02 (0.96)	8.00 (0.16)	1.0	2	0.603
Egg score (rank)	2.31 (0.08)	1.85 (0.07)	2.43 (0.13)	24.8	2	<0.001

[a] Male age and egg score are χ^2-values; all others are *F*-values

[b] In the case of the *F*-statistics, the *df* represents the independent variable nest position followed by the error term

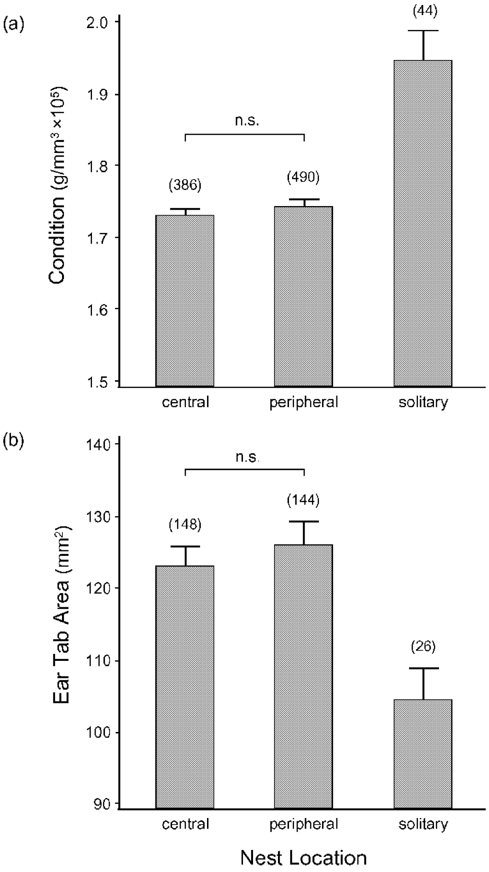

Fig. 1 The differences among central, peripheral and solitary males in **a** condition and **b** ear tab area. The *horizontal lines* denote homogeneous subsets that were identified using Tukey post hoc tests (see text)

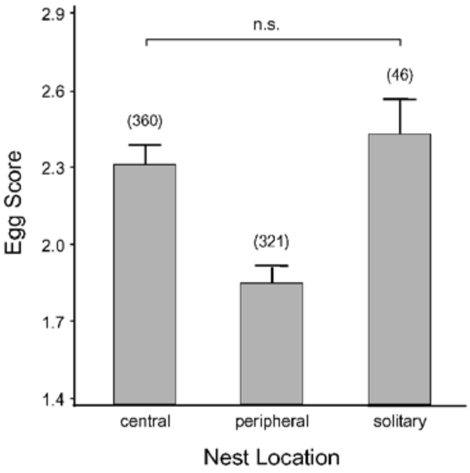

Fig. 2 The differences among central, peripheral and solitary males in egg scores. The *horizontal line* denotes a homogeneous subset that was identified using Mann-Whitney *U* tests (adjusted for multiple comparisons; see text)

n=144), but not for solitary males (r^2=0.07, P=0.182, n=26) (Fig. 3). For central males the power function was ear tab area =0.001 × body length$^{2.18}$ and the 95% confidence interval in the exponent was 1.28–3.08; for peripheral males the power function was ear tab area =0.0001 × body length$^{2.64}$ and the 95% confidence interval in the exponent was 1.78–3.50; for solitary males the power function was ear tab area = 0.285 × body length$^{1.12}$ and the 95% confidence interval in the exponent was −0.56–2.81. There was no significant difference between any of the exponents (t-test: P>0.05 for each comparison).

Of the 901 tagged males, 119 (13%) nested a second time during a single breeding season (Table 3). Seven of 115 males (6%) that nested colonially in their first breeding attempt switched to nest solitarily in their second breeding attempt, and none of the 4 males (0%) that nested solitarily in their first breeding attempt switched to nest colonially. The chi square analysis indicated that there was a significant degree of consistency (χ^2=40.6, df=1, P<0.001).

Discussion

It has been proposed that brood predation may be the driving force behind the evolution of coloniality in bluegill (Dominey 1981; Gross and MacMillian 1981). However, benefits such as mobbing behavior of predators will trade-off with costs such as increased cuckoldry that occurs in colonies. When the costs of nesting colonially

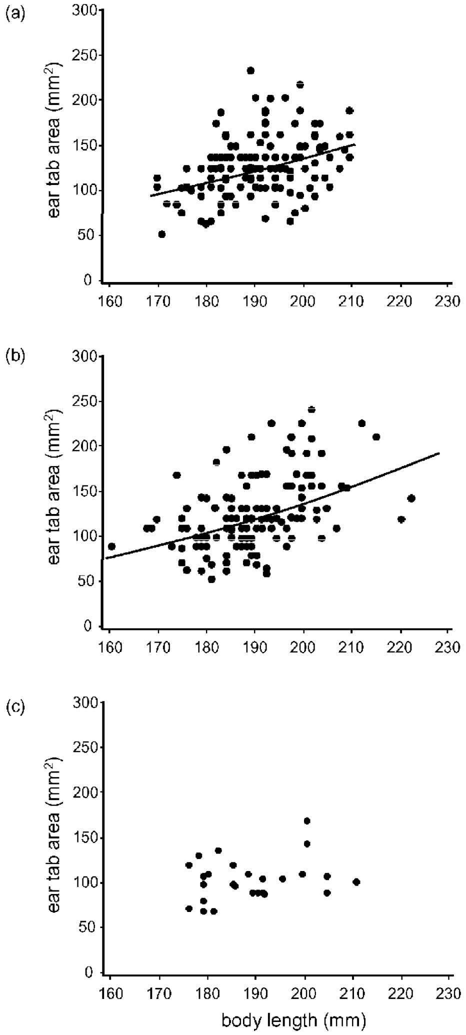

Fig. 3 The relationship between body length and ear tab area for **a** central, **b** peripheral, and **c** solitary males (non-significant). Statistical analysis was performed on logarithm transformed values. The data are presented untransformed for clarity

Table 3 Summary of renesting data for 119 males

	Second spawning		
First spawning	Central	Peripheral	Solitary
Central	29	21	2
Peripheral	22	36	5
Solitary	0	0	4

exceed the benefits, individuals will maximize their fitness by instead nesting solitarily. In this study we found that 4.5% of parental male bluegill nested solitarily, and these males were in better condition but had smaller ear tabs than colonial nesting males. Solitary males also obtained as many eggs as the most successful colonial males. We suggest that to nest solitarily is either a facultative decision made based on individual condition just prior to nesting or a life history decision made some time prior to maturation.

Bluegill females do not appear to discriminate against solitary nesting males. Solitary parentals obtained similar numbers of eggs to centrally located colonial parentals, and both these male types obtained more eggs than peripherally located colonial males (Fig. 2). Similar results were also observed in the closely related, colonially breeding longear sunfish *L. megalotis* (Jennings and Philipp 1992). Furthermore, within both bluegill and longear sunfish colonies there was no relationship between mean egg number per nest and the number of nesting males, suggesting that females do not prefer larger colonies. It is possible that our egg scores underestimated the number of eggs spawned in solitary nests because egg predation rates are higher in solitary nests than colonial nests and we took our egg scores the day after spawning. However, most egg predation occurs from other sunfish, which do not actively feed during the night hours (Gross and MacMillian 1981).

The female mating patterns in bluegill and longear sunfish are in contrast to those reported in the coral reef fish *A. abdominalis*. Unlike in sunfish, female *A. abdominalis* preferred males in larger colonies than those in smaller colonies (Tyler 1995). Larger colonies in *A. abdominalis* afford greater protection from predation, while in sunfish, density of nesting males appears more important than number (Gross and MacMillian 1981). In both cases there is a cost of cuckoldry. It is possible that predation pressure on coral reefs is significantly higher than in the freshwater lakes and streams in which the sunfish are found. Thus, the benefit of reduced predation pressure in *A. abdominalis* may exceed any cost of increased cuckoldry and may promote female choice for colonial nesting and particularly for larger colonies. Indeed, male *A. abdominalis* do not appear to nest solitarily.

Solitary male bluegill had significantly smaller ear tabs than colonial males, suggesting that solitary males are under less intense intrasexual selection. Interestingly, we did not find a difference in the sizes of ear tabs of central and peripheral nesting males, despite the fact that central nest locations are more strongly contested because they are preferred by females. Ear tab size is clearly involved in male–male competition. In captivity, male bluegill rank in dominance hierarchies increased with ear tab size, once the effect of body size was removed (Ehlinger 1999). In addition, in a previous study using a different sampling method, central males were found to have significantly larger ear tab areas than peripheral males (Côté 1993). These observations support the notion that large ear tabs are important in male–male competition for high-quality nest sites. It is possible that males with smaller ear tabs nesting on the periphery abandoned their nests before we collected them (i.e., shortly after spawning), thus explaining the discrepancy with earlier studies.

In bluegill, only parentals in top energetic condition may be able to nest solitarily. Based on Fulton's condition factor, an index that correlates with lipid content in fish (Sutton et al. 2000; Neff and Cargnelli 2004), we found that solitary parentals were in better condition than colonial parentals (Fig. 1). There was no difference in body length or age of solitary and colonial parentals (Table 2). Solitary males must be more vigilant than colonial males and they must also fan their eggs more to prevent fungal infection (Gross and MacMillian 1981; Côté and Gross 1993). Because parentals do not forage during the care period, only males with high energy reserves prior to spawning might be capable of nesting solitarily.

Nesting solitarily may therefore represent a condition-dependent decision made at the onset of breeding each year, or a discrete life-history strategy available to the highest-quality individuals. It is unlikely, however, that solitarily nesting males are making the "best of a bad situation" (Howard 1978; Eberhard 1982) brought about by their competitively inferior ear tabs. First, solitary parentals were not smaller or younger than colonial parentals, but they were in better condition. Second, solitary males typically do not establish their nests synchronously with colonial males (i.e., on the same day), suggesting that solitary males are choosing their nest position rather than being excluded from colonies (Côté, unpublished data). Third, females did not discriminate against solitary parentals as measured by our egg scores. Thus, solitary parentals do not appear to be inferior to colonial parentals.

We cannot at present determine whether solitary nesting is a facultative or a life-history decision. Tracking data revealed consistency in a male's nesting tactic (colonial versus solitary) with less than 6% of males switching tactics between nesting attempts within a year (Table 3), which could support either interpretation of solitary nesting. The extent to which parental male body condition is determined by environmental versus genetic factors in bluegill is unknown. We did find significant variation in body condition among years, which suggests a large environmental influence. If solitary nesting is a facultative decision, we would predict that the seven individuals that switched from colonial to solitary nesting (see Table 3) improved in condition between spawning attempts, while all of the others did not. Unfortunately, we did not measure the condition of our repeat spawners on their second spawning attempt. A heritability study of nesting tactic (e.g., Brown and Brown 2000; Møller 2002) or an experimental manipulation of male condition could reveal the true nature of solitary nesting.

In conclusion, solitary nesting males in bluegill sunfish were similar in size and age to colonial nesting males, but were in better condition. Although solitary males had smaller ear tabs, females did not appear to discriminate against them. There was consistency in a male's nesting tactic, although we cannot yet determine if solitary and colonial nesting is a facultative or life-history decision.

Acknowledgements We thank Mart R. Gross, Trevor E. Pitcher, Marlene Zuk and the anonymous reviewers for helpful comments and discussion. Parts of this work were conducted at the Queen's University Biological Station. We thank Frank Phelan and Floyd Connors for logistical assistance. The work conformed to protocols outlined by the Canadian Council on Animal Care and was supported by the Natural Science and Engineering Research Council of Canada.

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