

Temporal Variation in Decisions about Parental Care in Bluegill, *Lepomis macrochirus*

Sarah E. Magee & Bryan D. Neff

Department of Biology, University of Western Ontario, London, ON, Canada

Correspondence

Bryan D. Neff, Department of Biology,
University of Western Ontario, 1151 Richmond
Street N, London, ON, Canada N6A 5B7.
E-mail: bneff@uwo.ca

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Abstract

Parental investment theory states that an individual will trade-off present and future reproductive potential to maximize lifetime reproductive success. Only when parental care is costly in terms of reduced future reproductive potential should individuals be sensitive to changes in the value of current offspring and adjust their care. Here, we examine temporal variation in parental care decision-making in bluegill (*Lepomis macrochirus*), in which care is provided by males called 'parentals'. Previous research has shown that parentals that nest early in the breeding season are in higher energetic condition than those that nest later, and early nesting males appear not to pay an opportunity cost to their care in terms of reduced future reproductive potential. Early nesting males also may have higher paternity in their broods than later nesting males. To examine the parental care decisions made by early and mid-season nesting parentals, we experimentally reduced males' perceived paternity by swapping eggs between nests. We found that experimental males that nested early in the breeding season adjusted their brood defence behaviour similarly to control males, which had sham egg swaps performed. Conversely, experimental males that nested mid-season significantly decreased their brood defence behaviour after the manipulation as compared with control males. Thus, unlike mid-season nesting males, early nesting males appear relatively insensitive to changes in brood value (paternity), possibly because early nesting males pay little cost in terms of reduced future reproductive potential to providing full care or because these males have a predisposition to high paternity.

Introduction

Behavioural ecologists have long been interested in the associations between parents and their offspring, and particularly in the care that parents provide to their young (Trivers 1972; Williams 1975). Trivers (1972) defined parental investment as the amount of care a parent provides to a current brood at the cost of future reproductive potential. This definition implies that there is an energetic cost to parental investment that leads to a trade-off between current and future reproduction (i.e. an opportunity cost to

care; also see Williams 1975; Sargent & Gross 1985; Westneat & Sherman 1993). As a consequence of this trade-off, parents are expected to decrease their level of care for current offspring whenever the value of future offspring has the potential of being greater. Alternatively, when care is not costly in terms of reduced future reproductive potential, parents are not expected to adjust their care for a current brood based on changes in offspring value.

A few studies have demonstrated that parents adjust their care behaviour only when there is an opportunity cost of reduced future reproductive

potential to providing that care (reviewed by Magrath & Komdeur 2003). For example, Székely & Cuthill (2000) studied Kentish plovers (*Charadrius alexandrinus*) and found that unlike females nesting early in the breeding season, females nesting late in the breeding season had limited re-mating opportunities. Thus, females nesting late in the breeding season had a low opportunity cost of care, whereas females nesting early in the breeding season had a high opportunity cost of care. Consequently, experimental manipulations of clutch size only affected the amount of parental care provided by females nesting early in the breeding season. In a second study, Balshine-Earn & Earn (1998) manipulated the opportunity cost of care by altering the operational sex ratio in Galilee St Peter's fish (*Sarotherodon galilaeus*). They found that in trials with a male biased sex ratio, only females showed an increase in their probability of abandoning a current brood. Conversely, in trials with a female biased sex ratio, only males showed an increase in their probability of abandoning a current brood.

Here, we examine temporal variation in parental care decisions in bluegill (*Lepomis macrochirus*). Previous research has shown that male bluegill that nest early in the breeding season appear not to have an opportunity cost of providing care (Cargnelli & Gross 1997; Cargnelli & Neff 2006). Specifically, Cargnelli & Neff (2006) tracked males throughout the breeding season and found that during first nesting attempts early in the breeding season, there was no relationship between the number of days males provided care and the probability of re-nesting. For those males that did re-nest, there was no relationship between the number of days they provided care and the time between completion of their first nest and the initiation of their second nest. Conversely, when these males nested again during the middle of the season, males that provided care for more days were less likely to re-nest during the late part of the season, and for those that did re-nest, there was a positive relationship between the number of days males provided care and the time between nesting attempts. Thus, these data suggest that early in the season there is a lower opportunity cost to providing care than during the middle part of the breeding season. Indeed, two previous studies of bluegill found that males that nested during the middle of the breeding season adjusted their parental care in response to experimental manipulations of brood value (Coleman et al. 1985; Neff 2003). Cuckoldry rates also may vary across the breeding season and they appear to be lower during the early part of the

season (mean paternity early in the season was $88 \pm 10\%$ [SD] while during the middle of the season it was $73 \pm 17\%$; B. D. Neff, unpublished data). This seasonal variation may predispose early nesting males to high paternity (Neff & Sherman 2002).

Here, we examine the parental care decisions of male bluegill nesting during both the early and middle parts of the breeding season. We experimentally reduced males' perceived paternity by swapping eggs between nests. Our experimental manipulation was not revealed to the males until after the eggs hatch when an odour cue of paternity released by the fry becomes available; previous research has shown that parental males cannot differentiate between eggs they fertilized and eggs fertilized by another male, but they can differentiate between water conditioned with newly hatched larvae that they fertilized and water conditioned with unrelated larvae (Neff & Sherman 2003, 2005). We compared the brood defence behaviour of experimental males to control males that were subjected to sham egg swaps. We predicted that only males breeding during mid-season would be sensitive to our manipulation of brood value (i.e. paternity) because only these males appear to pay an opportunity cost of care and because early nesting males may have a predisposition to high paternity.

Methods

Bluegill Reproductive Biology

Bluegill are endemic to, and common throughout, North America (Lee et al. 1980). Male bluegills have two distinct life histories termed 'parental' and 'cuckolder'. In Lake Opinicon, Ontario (44°34'N, 76°19'W), parentals mature at approx. 7 yr of age, court females and provide sole parental care (Gross & Nowell 1980). Cuckolders mature at 2 yr of age and then steal fertilizations from parentals using one of two tactics termed 'sneaker' and 'satellite' (Gross 1982). Sneakers are young cuckolders (age 2–3 yr) and they spawn by darting into a parentals nest during a female's egg release. Once sneakers reach approx. 4 yr of age, they change tactics and become satellites (Gross 1982). Satellites are the size of small females and mimic a female's morphology and behaviour (Gross 1982; Neff & Gross 2001). Females follow a single life history maturing at the age approx. 4 yr.

Bluegill spawning typically occurs annually between the months of May and Jul. Parentals nest in colonies and then spawn synchronously

throughout the season in what are termed 'bouts'. A bout begins when colonies form within the littoral zone of the lake. Colonies contain up to 300 nests, and competition occurs between parentals for preferred nest sites in the centre of the colony (Cargnelli & Gross 1996). Parentals use their caudal fin to sweep out a shallow, circular depression to form their nest. Females then approach a colony in a school and enter parentals' nests to spawn. A female may spawn with more than one parental, and her eggs are sometimes fertilized by cuckolders (approx. 21% of all eggs spawned in bluegill nests are sired by cuckolders; Neff 2001). Spawning in a colony typically lasts a single day.

Parentals provide sole care for the developing offspring; females and cuckolders leave the colony after spawning and presumably return to deeper waters to forage and replenish their energy reserves. The care period lasts up to 10 d and has two distinct stages. The egg stage typically lasts 2–3 d and parental care involves defence of the brood and fanning of eggs, presumably to actively maintain oxygen levels around the developing young (Tinbergen 1951; van Iersel 1953, p. 38). After the eggs hatch, the fry are guarded until they leave the nest 4–7 d later; the length of the care period decreases during the breeding season, likely because of the associated increase in water temperature and developmental rate (Cargnelli & Neff 2006). The care is essential for offspring survival; if a male abandons his nest during the care period, the offspring are quickly consumed by predators (e.g. pumpkinseed, *Lepomis gibbosus*). Parentals rarely leave the nest area for more than a few seconds. Consequently, they do not forage and lose an average of 11% of their body weight during the care period (Coleman & Fischer 1991; also see Rios-Cardenas & Webster 2005). Because of active fanning, the egg stage is the most energetically demanding with parentals typically losing approx. 75% of their total weight loss during this stage of the care period (Coleman & Fischer 1991). After the eggs hatch, parentals are able to assess their paternity based on a direct, olfactory cue of relatedness released by the newly hatched fry (Neff & Sherman 2003, 2005). Once the fry leave the nest, parentals return to deeper water to forage and replenish their energy reserves before nesting again. Males may nest as many as three times during the breeding season and males that nest in the early part of the season are larger than those that nest later in the season (Cargnelli & Neff 2006). Larger males also emerge from winter in better energetic condition as measured by neutral and membrane-bound polar lipid content

(Cargnelli & Gross 1997) and thus, nesting during the early part of the season appears to be limited to males in high energetic condition. Fewer females breed early in the season and consequently, brood sizes early in the season are only approx. half the size of those spawned during the middle of the season (Cargnelli & Gross 1996; Cargnelli & Neff 2006).

Perceived Paternity and Parental Care

Two colonies were selected, one in the first 'trimester' of spawning (6–17 Jun.; $n = 23$ males) and the other in the second 'trimester' of spawning (18–29 Jun.; $n = 25$ males; the breeding season can be divided into three periods of equal duration, which we refer to as trimesters). For each colony, the day after spawning, we assigned egg scores as a rank between 1 (eggs covering 20% of nest) and 5 (eggs covering 100% of nest). The scores have been shown to be highly correlated with the actual number of eggs: score 1, 27–4889 eggs; score 2, 4666–28 806; score 3, 27 072–53 221; score 4, 49 369–86 552; and score 5, 82 063–112 810 ($r = 0.96$, $n = 32$, $p < 0.001$; Claussen 1991). Pairs of nests with equal egg scores were then alternately assigned to one of two treatment groups, control or experimental, and individually marked with a numbered tile placed at the nest edge. We then collected the pairs of parentals using dip nets and took them to a nearby boat where they were tagged with a t-bar Floy tag through the tissue just below the dorsal fin, weighed and measured for total length. While parentals were on the boat we swapped approx. half of the eggs between the paired experimental nests, or performed sham swaps on control nests by removing half the eggs and then shortly afterwards replacing them back into the same nest (see Neff 2003). Eggs were handled with a scoop and care was taken to minimize the amount of substrate collected with the eggs. Collected eggs were placed into a plastic container prior to moving them between nests or to placing them back into the source nest. After the manipulations were completed, males were released in close proximity to their nests where they resumed parental care.

The day following egg manipulation (the second day post-spawning), parental care was measured as a function of brood defence by presenting a live brood predator (pumpkinseed) in a plastic bag at the edge of each parental's nest (Coleman et al. 1985; Neff 2003). The predator [average size = 155 ± 10 mm (SD)] was presented twice for 30-s intervals with a 30-s interval in between. During the two, 30-s intervals, defence was measured by counting the number

of lateral displays, opercular flares and bites directed towards the predator. Brood defence was calculated from an overall index according to $1 \times$ lateral displays + $2 \times$ opercular flares + $3 \times$ bites. The coefficients were selected to reflect the relative intensity (i.e. level of aggression) of each of the three behaviours (Colgan & Gross 1977). Brood defence was tested two more times, 1 and 2 d post-hatching. These latter two scores were correlated ($r > 0.54$, $p < 0.01$ for both colonies) and averaged to provide a single measure of post-hatching defence. We assumed that our egg swaps would be revealed to the experimental parentals only after the eggs hatched when the olfactory cue of relatedness becomes available (Neff & Sherman 2003, 2005).

Fulton's condition factor was calculated from weight/length³ as an estimate of each male's energetic state (Sutton et al. 2000; Neff & Cargnelli 2004). We used length and Fulton's condition factor but not weight in subsequent analyses because length and weight are highly correlated and the residual weight is captured in the Fulton's index (Neff & Cargnelli 2004). Parentals that abandoned during the care period were given brood defence scores of 0 in all subsequent defence trials. All statistical analyses were run using SPSS (v. 12.0; SPSS Inc., Chicago, IL, USA).

Results

First Trimester

There were 23 nesting parentals in our first trimester colony at the time of spawning that subsequently underwent egg manipulations with 11 experimental

and 12 control nests. One experimental male abandoned his nest after the eggs hatched, while no control males abandoned their nests. Parentals provided a total of 10 d of care including 3 d of fanning before hatching occurred. A repeated measures ANOVA revealed that experimental and control males increased their level of defence between the pre- and post-hatching stages of care (Table 1; Fig. 1). Because the interaction effect between stage of care and treatment was not significant, both types of males increased their defence similarly between the two stages. Overall, experimental and control males provided similar levels of defence (sum of defence scores: experimental, 102 ± 16 SE; control, 102 ± 10 SE).

Independent samples t-tests revealed no significant difference between experimental and control males in body length ($t_{21} = 2.02$, $p = 0.057$), Fulton's condition factor ($t_{21} = 0.53$, $p = 0.60$) or egg score ($t_{21} = 0.64$, $p = 0.53$; Table 2). There also was no relationship between these variables and the level of defence provided pre- or post-hatching or the change in defence across the two stages (Table 3).

Second Trimester

There were 25 nesting parentals in our second trimester colony at the time of spawning that subsequently underwent egg manipulations with 13 experimental and 12 control nests. One experimental male and one control male abandoned their nests after the first defence measure and two additional experimental males abandoned after the eggs hatched and between our second and third defence measures (i.e. we had one defence measure after the

Table 1: Summary of repeated measures ANOVA results for brood defence of parental male bluegill (*Lepomis macrochirus*)

Colony ^a	Variable	ss	df	F	p
First trimester	Stage of care (repeated measure)	6588.5	1,21	14.6	0.001
	Treatment	13.8	1,21	0.016	0.900
	Stage of care \times treatment	137.3	1,21	0.304	0.587
	Error	17714.5	21		
Second trimester	Stage of care (repeated measure)	1352.8	1,22	6.63	0.017
	Treatment	1140.5	1,22	1.24	0.277
	Stage of care \times treatment	2184.6	1,22	10.7	0.003
	Length (covariate)	7115.6	1,22	7.75	0.011
	Stage of care \times length	1337.7	1,22	6.56	0.018
	Error	4488.9	22		

Analyses were performed on males nesting during either the first or second trimester of the breeding season.

ss, sum-of-squares; df, degrees of freedom (numerator, denominator).

^aLength was included as a covariate for the second trimester colony to control for differences in body size between control and experimental males; inclusion of length as a covariate in the first trimester analysis had no effect on the results.

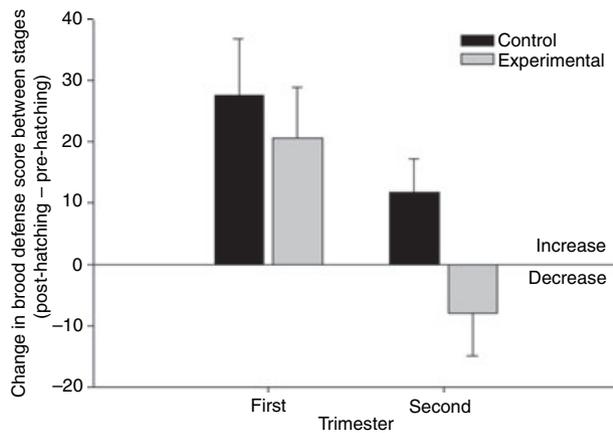


Fig. 1: Changes in brood defence score between pre- and post-hatching stages of the nesting period for parental male bluegill (*Lepomis macrochirus*). Bars represent control or experimental males nesting during either the first or second trimester. Brood defence score is an index of the aggressive response of a male to the presentation of a potential brood predator. The change was calculated as brood defence score during the post-hatching stage of care minus the score during the pre-hatching stage of care. Positive values therefore represent an increase in defence during the care period, whereas negative values represent a decrease in defence. Error bars represent 1 SE

Table 2: Summary of mean length, Fulton's condition factor and egg score for parental male bluegill (*Lepomis macrochirus*)

	Control			Experimental		
	n	\bar{x}	SE	n	\bar{x}	SE
First trimester						
Length	12	196.3	1.7	11	190.7	2.2
Fulton's	12	1.97	0.04	11	1.94	0.04
Egg score	12	1.67	0.14	11	1.55	0.13
Second trimester						
Length	12	198.3	1.9	13	192.2	2.1
Fulton's	12	1.88	0.04	13	1.87	0.03
Egg score	12	3.42	0.29	13	3.88	0.23

Data are displayed for control and experimental males breeding in either the first or second trimester of the season.

n, number of males.

eggs hatched for both these latter males). Parentals provided a total of 8 d of care including 3 d of fanning before hatching occurred. For this colony, we included body length as a covariate in the repeated measure ANOVA because we found that there was a significant difference in the length of experimental and control males (control males were longer than experimental males; $t_{23} = 2.19$, $p = 0.039$; Table 2) and there was a negative trend between males' length and their level of defence (Table 3). The ANOVA revealed that there was no significant differ-

ence in the overall levels of defence provided by experimental and control males (sum of defence scores: experimental, 120 ± 14 SE; control, 78 ± 14 SE; Table 1). However, experimental and control males changed their level of defence between the pre- and post-hatching stages of care and, as indicated by the significant interaction between the stage of care and treatment, control males increased their level of defence while experimental males decreased their level of defence (Fig. 1). Specifically, control males increased their defence by 36% while experimental males decreased their defence by 12%. The covariate length had a significant effect on defence with smaller males providing a higher level of defence (Tables 1 and 3). The significant interaction between stage of care and length indicated that the correlation between length and level of defence differed between the two stages; there was a stronger negative relationship between these two variables post-hatching than pre-hatching (see Table 3). The three-way interaction between stage of care, treatment and length was not significant ($p = 0.87$) and was removed from the final model. Similar results were found when the repeated measure analyses were performed with the subset of males that did not abandon their nest or when principle components analyses were used to combine the three behavioural responses (i.e. lateral display, opercular flare, and bites) into a single index (see Appendix 1).

Independent samples t-tests revealed no significant difference between experimental and control males in Fulton's condition factor ($t_{23} = 0.24$, $p = 0.81$) or egg score ($t_{23} = 1.30$, $p = 0.21$). Furthermore, there was no relationship between these variables and the level of defence provided pre- or post-hatching or the change in defence across the two stages (Table 3).

Colony Comparisons

There was no significant difference in the body length of males from the two colonies ($t_{46} = 0.74$, $p = 0.46$; Table 2). However, males from the first trimester were in better condition than males from the second trimester ($t_{46} = 2.17$, $p = 0.035$). Egg scores also differed significantly between colonies with males from the second trimester having a higher egg score than males from the first trimester (Mann-Whitney $U = 25.5$, $n = 48$, $p < 0.001$). Finally, males from the two colonies provided a similar level of defence (sum of defence scores: first trimester, 102 ± 9 SE; second trimester, 100 ± 10 SE; $t_{46} = 0.13$, $p = 0.90$).

Table 3: Summary of Spearman's correlation coefficients comparing length, Fulton's condition factor and egg score to three measures of brood defence for parental male bluegill (*Lepomis macrochirus*)

	Control			Experimental				
	n	Pre-hatching	Post-hatching	Change in defence	n	Pre-hatching	Post-hatching	Change in defence
First trimester								
Length	12	0.360	-0.210	-0.370	11	-0.339	-0.174	0.059
Fulton's	12	0.515	-0.046	-0.308	11	-0.164	-0.109	0.255
Egg score	12	-0.180	-0.282	-0.154	11	0.258	0.197	-0.140
Second trimester								
Length	12	-0.106	-0.538	-0.629*	13	-0.307	-0.640*	-0.310
Fulton's	12	-0.070	0.154	0.196	13	0.269	0.489	0.187
Egg score	12	0.130	-0.175	-0.304	13	-0.280	-0.029	0.219

Data are displayed for control and experimental males breeding in either the first or second trimester of the season.

Change in defence was calculated as brood defence score during the post-hatching stage of care minus the score during the pre-hatching stage of care.

n, number of males.

* $p < 0.03$, but neither result was significant after a Bonferroni correction that set $\alpha = 0.006$; all other p -values were non-significant ($p > 0.05$).

Discussion

Trivers (1972) concept of parental investment assumes that energetic investment in current offspring comes at a cost of reduced future reproductive potential; a parent that invests more in present offspring will not be able to produce as many offspring in the future as an individual that invests less in present offspring. In bluegill, mid-season nesting parentals, but not early season nesting parentals, appear to experience such a cost of reduced future reproductive potential (Cargnelli & Neff 2006). Consistent with this seasonal variation in the opportunity cost of care, we found that only mid-season nesting parentals changed their level of brood defence in response to changes in brood value (paternity). Early nesting parentals were insensitive to the same manipulation.

In bluegill, providing care during the early part of the breeding season may require less energy than later in the season. For example, we found that broods spawned in the first trimester colony were approx. half the size of those spawned in the second trimester colony (also see Cargnelli & Neff 2006) and smaller broods require less fanning, an energetically expensive component of parental care (Coleman & Fischer 1991). Furthermore, water temperatures are cooler earlier in the season, which will lead to a higher level of dissolved oxygen (Gerking & Lee 1980), and therefore early broods should require less fanning to supply eggs with sufficient oxygen for development than mid-season broods (also see Jones & Reynolds 1999; Lissåker et al. 2003). In addition, offspring from broods spawned early in the season have over twice

the survivorship to 1 yr of age than offspring from broods spawned mid-season presumably because of a longer pre-winter growing season (Cargnelli & Gross 1996). As such, although brood sizes are smaller early in the season, each offspring has greater value than those from mid-season broods.

Parentals nesting early in the breeding season also may have reduced metabolic costs. Temperature is an important environmental factor that influences the rate of physiological functions in fish including metabolism; as water temperatures increase, metabolic rates in fish also increase (Fry 1971; Burel et al. 1996). Thus, parentals that nest early in the season in colder temperatures pay a lower metabolic cost of care. In our study, males nesting during the first trimester experienced mean water temperatures of 20.3°C, while those nesting in the second trimester experienced mean water temperatures of 23.3°C. Using a temperature-metabolic rate relationship determined for bluegill (Dent & Lutterschmidt 2003), this 3°C increase in temperature corresponds to a 20% increase in metabolic rate. However, the parentals in our study that nested during the first trimester spent a total of 10 d providing care while those nesting during the second trimester provided only 8 d (albeit the two groups of males fanned for the same number of days). Thus, it is unclear if the reduced metabolic rates of early nesting males actually lead to a net reduction in expended energy during the care period.

There are alternative hypotheses that might explain the difference in sensitivity to changes in brood value that we observed between early and

mid-season nesting parentals. For example, it would be beneficial to track the same males throughout the breeding season because our early season nesting parentals may have had different future reproductive potential than our mid-season nesting parentals. If early nesting males were older than mid-season nesting males and less likely to survive to breed again, then they may invest all of their energy into parental care regardless of changes in brood value. However, in our study there was no significant difference in body length between early and mid-season nesting parentals suggesting that a difference in age is unlikely. It is also conceivable that the mechanism used to assess paternity (i.e. odour cue released by fry) is ineffective early in the season, either because of the smaller brood sizes, or because males breeding early in the season have predispositions about paternity. Such a predisposition could occur if cuckoldry rates were consistently lower early in the season than during the middle part of the season (Neff & Sherman 2002). We are currently examining seasonal variation in cuckoldry rates and a preliminary analysis suggests that cuckoldry rates are lower early in the breeding season than during the middle of the breeding season (see Introduction).

In conclusion, we found that care-providing bluegill males are sensitive to changes in the value of their current offspring during the middle of the breeding season, but not during the early part of the season. These results are consistent with data suggesting that there is a greater cost in terms of future reproductive potential to males providing care during the middle, but not early, part of the breeding season. The results are also consistent with a predisposition in early nesting males to high paternity because cuckoldry rates appear to be lower during this part of the season.

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Literature Cited

- Balshine-Earn, S. & Earn, D. J. D. 1998: On the evolutionary pathway of parental care in a mouth-brooding cichlid fish. *Proc. R. Soc. Lond. B.* **265**, 2217–2222.
- Burel, C., Person-Le Ruyet, J., Gaumet, F., Le Roux, A., Sévère, A. & Boeuf, G. 1996: Effects of temperature on growth and metabolism in juvenile turbot. *J. Fish Biol.* **49**, 678–692.
- 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*). *Can. J. Fish. Aquat. Sci.* **53**, 360–367.
- Cargnelli, L. M. & Gross, M. R. 1997: Fish energetics: larger individuals emerge from winter in better condition. *Trans. Am. Fish. Soc.* **126**, 153–156.
- Cargnelli, L. M. & Neff, B. D. 2006: When to breed: condition-dependent nesting in bluegill sunfish, *Lepomis macrochirus*. *J. Anim. Ecol.* **75**, 627–633.
- Claussen, J. E. 1991: Annual variation in the reproductive activity of a bluegill population: effect of clutch size and temperature. M.Sc. Thesis. Univ. of Toronto, Toronto.
- 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.
- Coleman, R. M., Gross, M. R. & Sargent, R. C. 1985: Parental investment decision rules: a test in bluegill sunfish. *Behav. Ecol. Sociobiol.* **18**, 59–66.
- Colgan, P. W. & Gross, M. R. 1977: Dynamics of aggression in male pumpkinseed sunfish (*Lepomis gibbosus*) over reproductive phase. *Z. Tierpsychol.* **43**, 139–151.
- Dent, L. & Lutterschmidt, W. I. 2003: Comparative thermal physiology of two sympatric sunfishes (Centrarchidae: Perciformes) with a discussion of microhabitat utilization. *J. Therm. Biol.* **28**, 67–74.
- Fry, F. E. J. 1971: The effects of environmental factors on the physiology of fish. In: *Fish Physiology*, Vol. 6 (Hoar, W. S. & Randall, D. J., eds). Academic Press, New York, pp. 1–98.
- Gerking, S. D. & Lee, R. M. 1980: Reproductive performance of the desert pupfish (*Cyprinodon n. nevadensis*) in relation to salinity. *Environ. Biol. Fish.* **5**, 375–378.
- Gross, M. R. 1982: Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol.* **60**, 1–26.
- Gross, M. R. & Nowell, W. A. 1980: The reproductive biology of rock bass, *Ambloplites rupestris* (Centrarchidae), in Lake Opinicon, Ontario. *Copeia* **1980**, 482–494.
- van Iersel, J. J. A. 1953: An analysis of the parental behaviour of the male threespined stickleback (*Gasterosteus aculeatus* L.). *Behaviour (Suppl.)* **3**, 1–159.

- Jones, J. & Reynolds, J. D. 1999: Costs of egg ventilation for male common gobies breeding in conditions of low dissolved oxygen. *Anim. Behav.* **57**, 181–188.
- Lee, D. S., Gilbert, C. R., Hocutt, C. H., Jenkins, R. E., McAllister, D. E. & Stauffer, J. R., Jr 1980: Atlas of North American Freshwater Fishes. North Carolina State Museum of Natural History, Raleigh.
- Lissåker, M., Kvarnemo, C. & Svensson, O. 2003: Effects of a low oxygen environment on parental effort and filial cannibalism in the male sand goby *Pomatoschistus minutus*. *Behav. Ecol.* **14**, 372–381.
- Magrath, M. J. L. & Komdeur, J. 2003: Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* **18**, 424–430.
- Neff, B. D. 2001: Genetic paternity analysis and breeding success in bluegill sunfish (*Lepomis macrochirus*). *J. Hered.* **92**, 111–119.
- Neff, B. D. 2003: Decisions about parental care in response to perceived paternity. *Nature*. **422**, 716–719.
- Neff, B. D. & Cargnelli, L. M. 2004: Relationships between condition factors, parasite load and paternity in bluegill sunfish, *Lepomis macrochirus*. *Environ. Biol. Fish.* **71**, 297–304.
- Neff, B. D. & Gross, M. R. 2001: Dynamic adjustment of parental care in response to perceived paternity. *Proc. R. Soc. Lond. B.* **268**, 1559–1565.
- Neff, B. D. & Sherman, P. W. 2002: Decision making and recognition mechanisms. *Proc. R. Soc. Lond. B.* **269**, 1435–1441.
- Neff, B. D. & Sherman, P. W. 2003: Nestling recognition via direct cues by parental male bluegill sunfish (*Lepomis macrochirus*). *Anim. Cogn.* **6**, 87–92.
- Neff, B. D. & Sherman, P. W. 2005: *In vitro* fertilization reveals offspring recognition via self-referencing in a fish with paternal care and cuckoldry. *Ethology* **111**, 425–438.
- Rios-Cardenas, O. & Webster, M. S. 2005: Paternity and paternal effort in the pumpkinseed sunfish. *Behav. Ecol.* **16**, 914–921.
- Sargent, R. C. & Gross, M. R. 1985: Parental investment decision rules and the Concorde fallacy. *Behav. Ecol. Sociobiol.* **17**, 43–45.
- Sutton, S. G., Bult, T. P. & Haedrich, R. L. 2000: Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. *Trans. Am. Fish. Soc.* **129**, 527–538.
- Székely, T. & Cuthill, I. C. 2000: Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. *Proc. R. Soc. Lond. B.* **267**, 2087–2092.

- Tinbergen, N. 1951: *The Study of Instinct*. Clarendon Press, Oxford, pp. 58–59.
- Trivers, R. L. 1972: Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Campbell, B., ed.). Aldine Press, Chicago, pp. 136–179.
- Westneat, D. F. & Sherman, P. W. 1993: Parentage and the evolution of parental behavior. *Behav. Ecol.* **4**, 66–77.
- Williams, G. C. 1975: *Sex and Evolution*. Princeton Univ. Press, Princeton, NJ.

Appendix 1: Summary of repeated measures ANOVA results for brood defence of parental male bluegill (*Lepomis macrochirus*). Analyses were performed on males nesting during either the first or second trimester of the breeding season and comprise: (1) omitting males that abandoned their nest prior to the end of the experiment; or (2) combining behavioural response variables using a principal components analysis (PCA).

Variable ^a	ss	df	F	p
First trimester, males that abandoned omitted				
Stage of care (repeated measure)	7593.6	1,20	17.9	<0.001
Treatment	287.5	1,20	0.408	0.530
Stage of care × treatment	18.0	1,20	0.042	0.839
Error	8470.8	20		
First trimester, PCA ^b				
Stage of care (repeated measure)	565.0	1,21	19.2	<0.001
Treatment	9.12	1,21	1.13	0.300
Stage of care × treatment	1.22	1,21	0.041	0.841
Error	617.7	21		
Second trimester, males that abandoned omitted				
Stage of care (repeated measure)	212.0	1,18	2.21	0.155
Treatment	2133.5	1,18	2.30	0.146
Stage of care × treatment	551.7	1,18	5.74	0.028
Length (covariate)	1727.2	1,18	1.87	0.189
Stage of care × length	184.8	1,18	1.92	0.182
Error	1728.6	18		
Second trimester, PCA ^b				
Stage of care (repeated measure)	12.1	1,22	1.43	0.244
Treatment	197.0	1,22	2.93	0.101
Stage of care × treatment	63.0	1,22	7.44	0.012
Length (covariate)	212.0	1,22	3.15	0.090
Stage of care × length	10.0	1,22	1.18	0.289
Error	186.3	22		

ss, sum-of-squares.

^aLength was included as a covariate for the second trimester colony to control for differences in body size between control and experimental males; there was no difference in body size between control and experimental males in the first trimester colony.

^bPCA loadings were for first trimester, lateral display = 0.061, opercular flare = 0.638, bites = 0.767, and for second trimester, lateral display = 0.096, opercular flare = 0.319, bites = 0.943.