

Increased performance of offspring sired by parasitic males in bluegill sunfish

Bryan D. Neff

Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada

Males of many species are characterized by alternative mating tactics. In bluegill sunfish (*Lepomis macrochirus*), some males delay maturation and become “parentals” while other males mature precociously and become “cuckolders.” Parentals use an overt, territorial mating tactic, defending a nest and courting females. Cuckolders instead use a sneaking tactic to parasitize parentals. It has previously been shown that parentals that are heavily cuckolded provide less care to their young, yet females do not appear to discriminate against cuckolders, and they may actually release more eggs when a cuckold is present than when spawning only with a parental. Here I examined growth rate of fry of known paternity through the yolk-sac stage of development using complementary laboratory and field studies to assess a potential indirect benefit for females that mate with cuckolders. Comparison of maternal half-siblings sired *in vitro* shows that cuckold offspring grow faster and to a larger size than parental offspring while feeding endogenously on their yolk sac. Because both food resource and maternal genes are equivalent across treatments, these data indicate a genetic difference in growth between the two male life histories. In the field, fry from nests that have proportionately more cuckold offspring are larger when they emerge from the nest. This increased size can lead to threefold higher survivorship for cuckold offspring than parental offspring from *Hydra canadensis* predation, a major predator of bluegill fry. These results are discussed in the context of mate choice for direct and indirect benefits and in the context of the evolution of alternative mating tactics. *Key words:* bluegill sunfish, good genes, growth rate, indirect benefits, *Lepomis macrochirus*, mate choice, mating systems. [*Behav Ecol* 15:327–331 (2004)]

Males of many species display alternative mating tactics (Brockmann, 2001; Gross, 1996; Henson and Warner, 1997; Taborsky, 1998). In fish, these alternative tactics have been broadly classified as a territorial “bourgeois” tactic, whereby a male attempts to monopolize access to a female, and a nonterritorial “parasitic” tactic whereby a male attempts to exploit the bourgeois male (Taborsky, 1997). Bourgeois males often provide parental care to the young in their territory and may reduce their care when parasitic males are successful at stealing fertilization during spawning (Trivers, 1972; Westneat and Sherman, 1993). In such cases, females pay a direct cost when their eggs are sired by parasitic males, and therefore females should avoid parasitic males when spawning.

Recent evidence from Atlantic salmon (*Salmo salar*) suggests that parasitic males have genes conferring a faster growth rate, at least during early development, than bourgeois males (Garant et al., 2002). Because growth rate is an important component of survivorship in fish (Miller et al., 1988; Toney and Coble, 1979), females might obtain an indirect benefit by mating with parasitic males (also see Garant et al., 2003). Furthermore, because males in Atlantic salmon provide no parental care, females should actually prefer to mate with parasitic males. In contrast, in mating systems where bourgeois males provide parental care, such as the bluegill sunfish (*Lepomis macrochirus*), a female would have to trade-off genetic benefits from parasitic males with reduced parental care by bourgeois males (*sensu* Alatalo and Rätti, 1995; Shellman-Reeve and Reeve, 2000). In this study I examined the genetic basis of growth rate in offspring of bourgeois and parasitic males of the bluegill sunfish as a potential indirect benefit for female mate choice.

Male bluegill are characterized by alternative mating tactics referred to as “parental” and “cuckolder” (Gross, 1982;

Gross and Charnov, 1980). In Lake Opinicon (southeastern Ontario; 44°16'N, 76°30'W), parentals mature at age 7 years and compete to construct nests in densely packed colonies during the breeding season (May–July). Nesting males court and spawn with females over the course of a single day and then provide sole parental care for the developing young in their nests (Gross, 1982). The care period last 7–10 days and involves fanning and defending the eggs until they hatch (2–3 days) and then defending the fry until they leave the nest (5–7 days). The care is critical for survival of the young. In contrast, cuckolders are parasitic males that mature precociously and steal fertilizations in the nests of parentals through two tactics: “sneakers” are young cuckolders aged 2–3 years that dart into nests during female egg releases; and “satellites” are older cuckolders aged 4–5 years that express female color and behavior and appear to deceive parentals into identifying them as a second female in the nest (Dominey, 1980, 1981; Gross, 1982; Neff and Gross, 2001). Cuckolders die before they ever reach the size of mature parentals, and there is no evidence that they ever become parentals themselves (Gross, 1982).

Nest-tending parentals that are cuckolded more provide less care to their young and are more likely to partially cannibalize or even abandon their brood (Neff, 2003; Neff and Gross, 2001). Thus, in bluegill, females pay a direct cost from cuckoldry. However, cuckolders are excellent sperm competitors, fertilizing some 80% of the eggs that females release when they successfully intrude into a parental's nest, and females do not appear to prevent intrusions (Fu et al., 2001). Furthermore, females may release up to three times as many eggs when a cuckold is present than when they spawn alone with a parental (Fu et al., 2001). This suggests that females may be exercising a cryptic form of choice (*sensu* Eberhard, 1996), preferring to mate in the presence of cuckolders.

In this study I examined the performance of offspring sired by parentals and cuckolders to determine if there is an indirect benefit for females that mate with cuckolders. Specifically, I

Address correspondence to B. D. Neff. E-mail: bneff@uwo.ca.

Received 16 October 2002; revised 13 May 2003; accepted 30 May 2003.

examined the growth rate and survivorship of fry using three approaches. First, I used maternal half-sibs sired *in vitro* to quantify the genetic contribution to growth rate from parentals and cuckolders. Growth rate was examined during the yolk-sac stage of development (i.e., before exogenous feeding). Thus, both parental and cuckolder offspring have equivalent energy sources from which to grow (the yolk sac from the egg), and any difference can be attributed to paternal genes (Barber and Arnott, 2000). Second, I used genetic markers to quantify natural rates of cuckoldry in the field and related this to the growth rate of parental and cuckolder offspring. Third, I quantified size-dependent predation on fry by *Hydra canadensis*, one of the most important predators on fry that emerge from the colony (Elliott et al., 1997).

METHODS

In vitro fertilization and growth rate

My assistants and I collected 18 fish (6 each of females, parentals, and cuckolders [4 sneakers and 2 satellites]) from a natural colony in Lake Opinicon shortly after spawning commenced in June 2000. Parentals were selected haphazardly from the colony, and cuckolders and gravid females were collected from the water column immediately above the colony. We collected eggs from each female by applying gentle pressure to the abdomen. Approximately equal numbers of eggs (40–50) were placed into two rearing dishes (1 l) containing 50 ml of water. A female was alternated between the two dishes twice during the collection so that about one-quarter of the eggs were placed into any one dish at a time.

We collected sperm from either a cuckolder or a parental using a 2-ml syringe (by applying gentle pressure to the gonad region) and used the sperm to fertilize the eggs. The life history of the first male was alternated in each successive trial. Males were used only once and females were used twice, once for a parental sample and once for a cuckolder sample. The sperm–egg–water mixture was left for 2 min, after which the dishes were filled with lake water. We placed a small air bubbler in each dish to ensure ample oxygen was present in the water. I conducted 30% water changes every 12 h at 0800 h and 2000 h each day. After 8 days, at the end of endogenous feeding, we collected the fry from each dish and preserved them in 70% ethanol.

My assistants later chose 10 fry haphazardly from each cross (120 fry total), and each fry was photographed using a digital camera. NIH imaging software was then used to calculate the total length of each fry. My assistants also measured the size of the eye by taking orthogonal measurements (length and width) intersecting the center of the eye. Eye area was calculated assuming the eye was an ellipse from the formula: $\pi \times \text{length} \times \text{width}$. I used eye area as another measure of body size and as an indication of visual acuity (Walton et al., 1994, 1997). The sire identity of each sample was unknown to the photographer and measurer. Following Welch et al. (1998), I used ANOVA with either body length or eye area as the dependent variable, sire life history (parental or cuckolder) as the independent variable, and family (i.e., mother's identification) as a random factor.

Cuckoldry and growth rate in the field

During the breeding season of 1999, my assistants and I collected a sample of 29 bluegill nests from colonies in Lake Opinicon and our experimental pool facility (see Fu et al., 2001). At the end of the care period (shortly before the fry "swim-up" and leave the nest), fry were uniformly sampled from not less than five places within each nest and preserved in 70% ethanol. We also took a small sample of the nest-

tending parental's caudal fin. We used microsatellite genetic markers to calculate each parental's paternity following methods outlined in Neff (2001). Because of the complex mating system, with multiple males and multiple females spawning in each nest, parent-offspring relationships could not be conclusively established. The parentage models instead identify proportions of young sired by each candidate parent (see Neff et al., 2000).

For up to 46 fry from each nest, my assistants measured body length and eye area as above and averaged the measurements. I examined the relationships between these averages and proportion of brood fertilized by cuckolders using linear regressions.

Size-dependent survivorship

My assistants and I quantified size-dependent survivorship of bluegill fry using *Hydra canadensis* as a predator. *Hydra* was selected because they kill an average of 20% of the fry that emerge from the colony (Elliott et al., 1997). We collected fry from seven nests during the breeding season of 2002, brought them back to the field laboratory, and placed them in 10 l aquariums. Each brood (nest) was kept together in its own aquarium, and once the fry began feeding exogenously (i.e., once they swim up off the bottom), they were fed frozen and fresh daphnia ad libitum. Broods were kept in aquarium for up to 10 days to provide fry of increasing body sizes.

We then collected *Hydra* from macrophytes (*Myriophyllum spicatum*) near the colonies from which the fry were originally collected. We placed 20 *Hydra* into each of 4 rectangular containers (20 × 15 × 10 cm) filled with 750 ml of lake water and left them for approximately 24 h at room temperature. The *Hydra* typically attached themselves to the sides or bottom of the container and began to forage by extending their tentacles. An additional four containers were also set up without *Hydra* to serve as controls.

A trial began at 1000 h EST when 20 fry (from the same brood) were introduced into each of the predator and control containers. The containers were left undisturbed for 24 h and were exposed to a natural light cycle (indirect light from a nearby window). We measured 10 other fry from the brood to the nearest 0.01 mm using a dissecting microscope with an ocular micrometer. We averaged these measurements to provide an estimate of the mean body size of the fry within the experimental containers. At the end of the 24-h period, we determined the number of fry consumed by *Hydra* by counting the number of black *Hydra* (indicative of fry consumption: Elliott et al., 1997) as well as the number of missing fry. These two counts were always consistent. We also counted and averaged the number of dead fry in the control containers. Survivorship was then calculated in each of the *Hydra* containers from (mean number of surviving fry in controls – number of fry consumed by *Hydra*) / mean number of surviving fry in controls. At the end of the trial we released all fry from the brood back into the lake. The experiment was repeated for a total of seven different broods and fry body sizes, and linear regression was used to compare the relationship between body length (logarithm transformed) and mean survivorship.

The density of fry and *Hydra* around colonies in Lake Opinicon at swim-up was estimated by Elliot and colleagues (1997) to be 22.5 and 25.5 per 750 ml, respectively. Thus, the densities in this experiment closely matched those found in nature.

All statistics were performed using SPSS (version 10). Analysis of variance utilized type III sums of squares. All means are reported plus or minus one standard error and all *p* values are from two-tailed tests.

RESULTS

In vitro fertilization and growth rate

For fry length, the ANOVA revealed a significant difference among families as well as a significant effect of sire life history (family: $F_{5,5} = 6.3$, $p = .03$; life history: $F_{1,5} = 10.7$, $p = .02$; family \times life history: $F_{5,108} = 1.7$, $p = .13$). Fry sired by cuckolders were longer than fry sired by parentals (Figure 1A). For fry eye area, the ANOVA revealed no difference among families, but a significant effect of sire life history (family: $F_{5,5} = 3.2$, $p = .11$; life history: $F_{1,5} = 9.4$, $p = .03$; family \times life history: $F_{5,108} = 1.8$, $p = .12$). Fry sired by cuckolders had larger eyes than fry sired by parentals (Figure 1B).

Cuckoldry and growth rate in the field

There was a positive relationship between the proportion of cuckold offspring in a nest and the average body length of the fry ($r^2 = .17$, $n = 29$, $p = .03$; Figure 2). From the regression, the mean length of parental offspring at swim-up (i.e., when they leave the nest) is predicted to be 4.37 mm ($Pr_c = 0$), and the mean length of cuckold offspring is predicted to be 5.29 mm ($Pr_c = 1$). Thus, cuckold offspring are predicted to be 21% longer ($= [5.29 - 4.37]/4.37$) than parental offspring when they leave the nest.

Although there was also a positive relationship between the proportion of cuckold offspring and the average eye area, this result was not significant ($r^2 = .10$, $n = 29$, $p = .10$).

Size-dependent survivorship

The mean number of fry that died within the control containers ranged from 0.5 to 4.75. There was no relationship between the mean number of fry that died and the mean fry size ($r^2 = .001$, $n = 7$, $p = .94$). Within the *Hydra* predation treatments, however, larger fry had significantly higher survivorship (Figure 3). Linear regression revealed a highly significant relationship between fry length and survivorship ($r^2 = .79$, $n = 7$, $p < .01$). The equation of the line was survivorship $= 3.83 \times \log_{10}(\text{length}) - 2.32$. Using this equation and the predicted sizes of parental (4.37 mm) and cuckold (5.29 mm) fry from the field, the survivorship is predicted to be 0.13 and 0.45 for the two types of offspring, respectively. Thus, cuckold fry are predicted to have over three times higher survivorship than parental fry ($0.45/0.13 = 3.46$).

From the *in vitro* fertilization experiment, parental fry were 5.15 mm and cuckold fry were 5.39 mm. Based on these data and the size-dependent survivorship equation above, the survivorship is predicted to be 0.41 and 0.48 for parental and cuckold offspring, respectively. Thus, in this case, cuckold fry are predicted to have 17% higher survivorship than parental fry ($0.48/0.41 = 1.17$). This latter calculation may be more reliable than the calculation based on the field data because it involves less extrapolation of the survivorship equation to a body size below the minimum tested (i.e., below 5.48 mm).

DISCUSSION

I have shown that the parasitic life history of bluegill sunfish (cuckolders) produce offspring that grow faster before exogenous feeding as compared with the parental life history. These differences can be attributed to paternal genetic effects (see Barber and Arnott, 2000). Thus, cuckold offspring appear inherently better able to metabolize nutrients in their yolk sac, converting them into somatic tissue. Increased growth

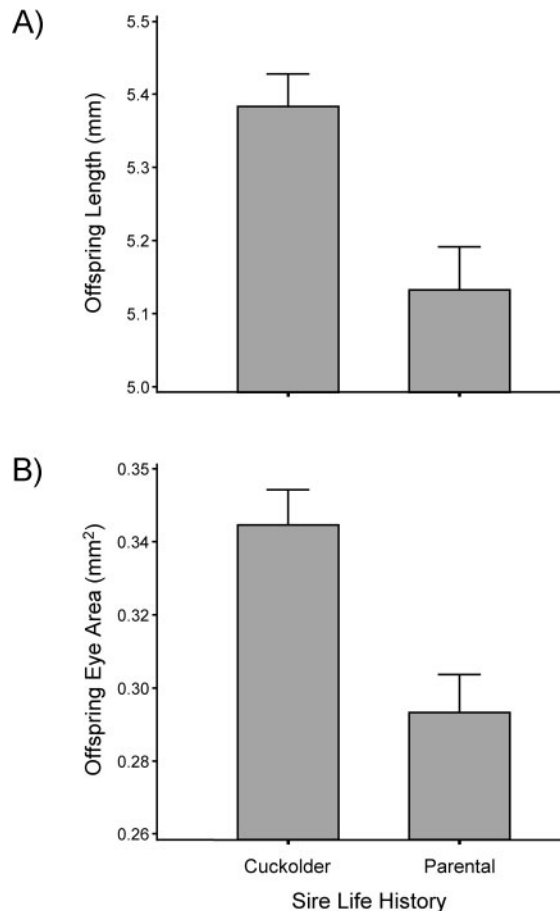


Figure 1
Summary of the *in vitro* fertilization experiment. Fry sired by cuckolders were on average 5% longer (A) and had 15% larger eyes (B) compared with fry sired by parentals. The bars represent averages (+SE) of all fry from each treatment ($n = 120$).

during early development is particularly important for survivorship in bluegill because fry experience strong size-dependent predation from *Hydra canadensis*. *Hydra* congregate on macrophytes around colonies and use stinging tentacles to capture prey. In Lake Opinicon, they are estimated to kill an average of 20% of the fry that emerge from the colony (Elliott et al., 1997). I have shown here that the increased size of cuckold offspring at the time they emerge from the colony may confer upward of a threefold increase in survivorship (estimated range 1.17–3.46) from *Hydra* predation alone.

Increased juvenile size can also increase survivorship through size-dependent feeding and starvation (e.g., Partridge and DeVries, 1999) and size-dependent overwinter mortality (e.g., Oliver et al., 1979; Toney and Coble, 1979). Miller and colleagues (1988) developed a general model for fish to estimate the probability of starvation based on body length. Using their model, the 21% increase in body size of cuckold offspring calculated here from the field data is predicted to lead to a 30% lower susceptibility to starvation. Cargnelli and Gross (1996) further showed that larger young-of-year can have considerably higher survivorship over the first winter as compared to smaller individuals. Thus, cuckold offspring may have considerably higher survivorship, at least during the first year of life.

It is unclear if the increased growth of cuckolders persists through to maturation. It is known that cuckolders grow

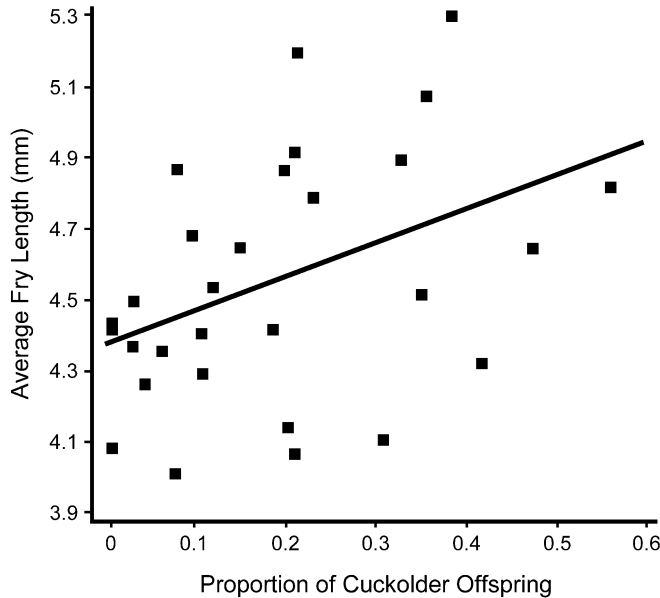


Figure 2
Regression analysis of cuckoldry rate and mean offspring length in the field. There was a positive relationship between the proportion of cuckolded offspring found in a nest and the average fry length.

slower after maturation than parentals of similar age (but still immature; Gross, 1982; Gross and Charnov, 1980). No doubt maturation is costly as cuckolders invest considerable energy into gonad development and mating effort, and this likely explains the difference (Gross, 1982). However, based on back calculations of growth from an analysis of scales, Gross (1982) was unable to detect a difference between growth rates of cuckolders and parentals. This may be because heritability of life history in bluegill is low or environmental variation dominates growth patterns, masking any genetic effect.

Three additional analyses could provide further insight into differences in growth and survivorship of parental versus cuckolder offspring. First, it is unknown if cuckolder and parental offspring have differences in their predation avoidance abilities independent of body size. The *Hydra* experiments used fry of known size, but of mixed parentage. Thus, it is possible that cuckolder offspring could be more or less susceptible to *Hydra* predation independent of their body size. Given that visual acuity increases with eye size (Walton et al., 1994, 1997) and that cuckolder offspring had larger eyes, it is conceivable that these individuals are better able to detect and avoid *Hydra* than parental offspring.

Second, the size of fry from the *in vitro* fertilization experiment differed from those predicted from the field data, independent of sire life history. Fry were larger in the laboratory experiment (cuckolder, 5.39 vs. 5.29 mm; parental, 5.15 vs. 4.37 mm). This variation may be attributed to differences in rearing temperature. The fry reared in natural nests experienced lower temperatures ranging from 17 to 22°C, while the fry reared in the laboratory were kept at room temperature, which ranged from 20 to 28°C. Dissolved oxygen concentrations in the water may also have contributed to the differences in size because the water in the *in vitro* experiment was actively aerated. Lower temperature and oxygen concentration are both known to reduce metabolic and growth rate (e.g., Claramunt and Wahl, 2000; Matschak et al., 1998), but the specific effects on the experiments conducted here are unknown.

Third, in the field cuckolders might preferentially spawn in

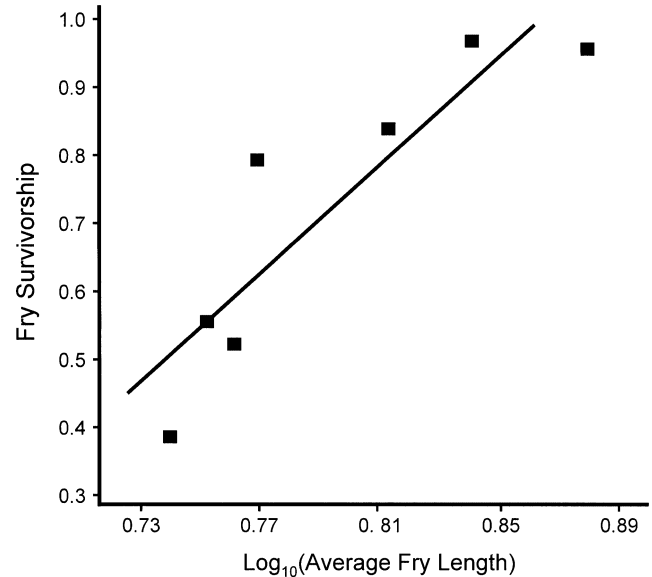


Figure 3
Size-dependent predation of *Hydra* on bluegill fry. Larger fry were less likely to be killed and consumed by *Hydra* under experimental conditions. Each data point represents an average of four trials.

nests that are in warmer water, have higher dissolved oxygen concentrations, or that attract higher quality females. Thus, on average, their offspring may experience better rearing conditions or benefit from greater maternal effects than parental offspring. This could contribute to the positive relationship found between cuckoldry rates and mean offspring size in natural nests. However, cuckoldry is known to reduce the fanning rate of nest-tending parental males (Neff and Gross, 2001), which could instead reduce growth rate of the developing young. It would be interesting to compare the size of parental offspring in nests with high versus low rates of cuckoldry. Nevertheless, the *in vitro* fertilization experiment clearly demonstrates a genetic basis to the difference in growth rate, albeit our analysis was based on a small sample of 12 sires.

In Atlantic salmon, Garant and colleagues (2002) found similar results, with offspring of precocious, parasitic males growing faster during the yolk-sac stage of development than offspring of the considerably larger anadromous males. They were able to rule out maternal effects because each brood was spawned by a single female but fertilized by multiple males. Ryan and colleagues (1992) also have suggested a genetic difference in growth rate between alternative life histories in swordtail fish. However, unlike the bluegill mating system, these other two systems do not have paternal care. Thus, in bluegill, spawning females must make complex choices between the potential genetic benefit of increased offspring growth obtained by mating with cuckolders and the direct benefit of increased paternal care obtained by mating with parental males. Females of many bird species have been shown to make similar choices trading off the direct benefit of paternal care from their social mate with genetic benefits obtained through extrapair fertilizations (Alatalo and Rätti, 1995; Johnsen et al., 2000; Shellman-Reeve and Reeve, 2000).

Finally, the data presented here could have consequences for understanding the evolution of alternative life histories. If the increased growth rate of cuckolder offspring confers higher survivorship to maturation, then parental offspring would have to have higher mating success to ensure equal fitnesses and

evolutionary stability of the alternative life histories (Maynard Smith, 1982). Conversely, the life histories might represent a condition strategy whereby higher quality individuals adopt the life history (and corresponding mating tactic) that confers higher fitness (Gross, 1996). In this case equal fitnesses are not required because all individuals in the population have the same “decision” gene, and the decision is made based on an individual’s status. The fact that cuckold offspring grow faster might lead to a greater proportion of them adopting the cuckold life history (see Hutchings and Jones, 1998). However, the parental life history would be maintained in the population through a combination of status and negative frequency-dependent selection (Gross, 1996; Hunt and Simmons, 2001). Although in bluegill it remains to be determined whether the alternative life histories represent a conditional strategy or alternative strategies, the predicted differential survivorship calculated here can be used in calculations of relative fitness (Gross and Charnov, 1980) and may help to understand the mechanism underlying the alternative life histories in bluegill.

I thank Joanna Lister, Michael Richards, and especially Peng Fu for field and laboratory assistance, Mart Gross and Paul Sherman for helpful discussion, and Rob Gegeer, Trevor Pitcher and three anonymous referees for helpful comments on the manuscript. Parts of this work were conducted at the Queen’s University Biological Station where Frank Phelan and Floyd Connor provided logistical support. The work conformed to guidelines of the Canadian Council on Animal Care and was supported by the Natural Sciences and Engineering Research Council of Canada.

REFERENCES

- Alatalo RV, Rätti O, 1995. Sexy son hypothesis—controversial once more. *Trends Ecol Evol* 10:52–53.
- Barber I, Arnott SA, 2000. Spit-clutch IVF: a technique to examine indirect fitness consequences of mate preferences in sticklebacks. *Behaviour* 137:1129–1140.
- Brockmann HJ, 2001. The evolution of alternative strategies and tactics. *Adv Study Behav* 30:1–51.
- Cargnelli L, Gross MR, 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.
- Claramunt RM, Wahl DH, 2000. The effects of abiotic and biotic factors in determining larval fish growth rates: A comparison across species and reservoirs. *Trans Am Fish Soc* 129:835–851.
- Dominey WJ, 1980. Female mimicry in male bluegill sunfish—a genetic polymorphism? *Nature* 284:546–548.
- Dominey WJ, 1981. Maintenance of female mimicry as a reproductive strategy in bluegill sunfish (*Lepomis macrochirus*). *Environ Biol Fish* 6:59–64.
- Eberhard WG, 1996. *Female control: sexual selection by cryptic female choice*. Princeton, New Jersey: Princeton University Press.
- Elliott JK, Elliott JM, Leggett WC, 1997. Predation by Hydra on larval fish: Field and laboratory experiments with bluegill (*Lepomis macrochirus*). *Limnol Oceanogr* 42:1416–1423.
- Fu P, Neff BD, Gross MR, 2001. Tactic-specific success in sperm competition. *Proc R Soc Lond B* 268:1105–1112.
- Garant D, Fleming IA, Einum S, Bernatchez L, 2003. Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecol Lett* 6:541–549.
- Garant D, Fontaine P-M, Good SP, Dodson JJ, Bernatchez L, 2002. The influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*). *Evol Ecol Res* 4:537–549.
- Gross MR, 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z Tierpsychol* 60: 1–26.
- Gross MR, 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol* 11:92–98.
- Gross MR, Charnov EL, 1980. Alternative male life histories in bluegill sunfish. *Proc Natl Acad Sci USA* 77:6937–6940.
- Henson SA, Warner RR, 1997. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annu Rev Ecol Syst* 28:571–592.
- Hunt J, Simmons LW, 2001. Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. *Proc R Soc Lond B* 268: 2409–2414.
- Hutchings JA, Jones MEB, 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can J Fish Aquat Sci* 55(Suppl):22–47.
- Johnsen A, Andersen V, Sunding C, Lifjeld JT, 2000. Female blue-throats enhance offspring immunocompetence through extra-pair copulations. *Nature* 406:296–299.
- Matschak TW, Tyler DD, Stickland NC, 1998. Metabolic enzyme activities in Atlantic salmon (*Salmo salar* L.) embryos respond more to chronic changes in oxygen availability than to environmental temperature. *Fish Physiol Biochem* 18:115–123.
- Maynard Smith J, 1982. *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- Miller TJ, Crowder LB, Rice JA, Marshall EA, 1988. Larval size and recruitment mechanisms in fishes: towards a conceptual framework. *Can J Fish Aquat Sci* 45:1657–1670.
- Neff BD, 2001. Genetic paternity analysis and breeding success in bluegill sunfish (*Lepomis macrochirus*). *J Hered* 92:111–119.
- Neff BD, 2003. Decisions about parental care in response to perceived paternity. *Nature* (in press).
- Neff BD, Gross MR, 2001. Dynamic adjustment of parental care in response to perceived paternity. *Proc R Soc Lond B* 268:1559–1565.
- Neff BD, Repka J, Gross MR, 2000. Parentage analysis with incomplete sampling of parents and offspring. *Mol Ecol* 9:515–528.
- Oliver JD, Holeton GF, Chua KE, 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Trans Am Fish Soc* 108:130–136.
- Partridge DG, DeVries DR, 1999. Regulation of growth and mortality in larval bluegills: implications for juvenile recruitment. *Trans Am Fish Soc* 128:625–638.
- Ryan MJ, Pease CM, Morris MR, 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*—Testing the prediction of equal fitnesses. *Am Nat* 139:21–31.
- Shellman-Reeve JS, Reeve HK, 2000. Extra-pair paternity as the result of reproductive transactions between paired mates. *Proc R Soc Lond B* 267:2543–2546.
- Taborsky M, 1997. Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviors? *Behav Ecol Sociobiol* 41:361–362.
- Taborsky M, 1998. Sperm competition in fish: “bourgeois” males and parasitic spawning. *Trends Ecol Evol* 13:222–227.
- Toneys ML, Coble DW, 1979. Size related first winter mortality of freshwater fishes. *Trans Am Fish Soc* 108:415–419.
- Trivers RL, 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man* (Campbell B, ed). Chicago: Aldine Press; pp. 136–179.
- Walton WE, Emiley JA, Hairston NG, 1997. Effect of prey size on the estimation of behavioral visual resolution of bluegill (*Lepomis macrochirus*). *Can J Fish Aquat Sci* 54:2502–2508.
- Walton WE, Easter SS, Malinoski C, Hairston NG, 1994. Size-related change in the visual resolution of sunfish (*Lepomis spp*). *Can J Fish Aquat Sci* 51:2017–2026.
- Westneat DF, Sherman PW, 1993. Parentage and the evolution of parental behavior. *Behav Ecol* 4:66–77.
- Welch AM, Semlitsch RD, Gerhardt HC, 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science* 280: 1928–1930.