

The Effect of an Experimental Brood Reduction on Male Desertion in the Panamanian Blue Acara Cichlid *Aequidens coeruleopunctatus*

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Abstract

Investment in present vs. future reproduction is a life-history trade-off faced by many animals. Because males generally pay a higher cost from lost mating opportunities than females, males are expected to react more strongly to changes in brood value. We examined the effect of an experimental brood reduction on male desertion in the substrate-brooding biparental cichlid *Aequidens coeruleopunctatus* under field conditions. We tested the prediction that brood reduction should decrease the duration of male care and examined the effect of brood reduction on the quality of male and female parental care. Our results show that males with reduced broods stopped providing parental care earlier than males with control broods. Males with reduced broods, however, also stayed longer with their broods as the season progressed. Brood reduction did not decrease daily investment in male or female parental care. We conclude that males trade off present and future reproduction by changing the duration but not the quality of parental care. The longer duration of male care in the experimental group later in the season suggests that the trade-off between present and future reproduction changes as the season progresses because the payoffs of desertion progressively decrease.

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Introduction

Selection should favor individuals that trade off present and future reproduction to maximize their lifetime reproductive success (Trivers 1972; Gross & Sargent 1985; Sargent & Gross 1986). One factor that may affect this tradeoff is the value of the current brood. Parents may assess this value by the size, quality, number and age of the offspring (Carlisle 1982; Clutton-Brock 1991). As the value of the current brood decreases, the opportunity cost or the gain from pursuing

additional matings increases relative to the expected benefits from providing further care. Parents should reduce their level of parental investment accordingly. In species in which males have a higher potential reproductive rate than females, males generally pay a higher cost from lost mating opportunities than females. Males are therefore expected to react more strongly than females to changes in brood value (Baylis 1981; Gross & Sargent 1985). Here we investigate how the value of a brood affects male desertion in the biparental Panamanian blue acara cichlid, *Aequidens coeruleopunctatus*.

In an extension to Maynard Smith's (1977) single-sex model of mate desertion, Lazarus (1990) developed a model in which individuals decide whether to stay or desert repeatedly during the parental care period, selecting the option that gives them the greater fitness and taking into account whether their mate has deserted. By deserting, individuals accrue a benefit, which is highest at the beginning of the parental care period and decreases to zero at the end of this period. One evolutionarily stable outcome of this model is that one parent deserts while the other one stays. This occurs when parents differ in the benefit from desertion, such as when males have a higher potential reproductive rate than females. In this case, males should desert when $V_1 + M > V_2$, where V_1 is the number of surviving young with uniparental care, M is the increment in male reproductive success by deserting, and V_2 is the number of surviving young with biparental care. Males should be less likely to desert when brood size is large because $V_1 + M$ generally does not exceed V_2 . However, as brood size decreases, V_1 and V_2 are both lowered relative to M . Under such conditions, $V_1 + M$ is more likely to exceed V_2 , thereby promoting male desertion.

Wisenden (1994) applied this model to the convict cichlid, *Cichlasoma (Archocentrus) nigrofasciata*, and found correlational support for his predictions. His results show that deserted broods were smaller than biparental broods under field conditions. However, this correlation could have arisen because males deserted broods that were small or because broods suffered increased predation when only one parent guarded them. An experimental manipulation of brood size is required to distinguish between these two explanations. We tested the model that males should desert when $V_1 + M$ exceeds V_2 in the cichlid *A. coeruleopunctatus*, a species in which male parental care varies widely. While some males stay with their broods until the young become independent, others desert their broods leaving the care to the females (Barlow 1974; Carlisle 1981, 1985; Vélez 1999). More specifically, we tested the prediction that brood reduction should decrease the duration of male care in pairs, where we either reduced brood size or left it unchanged.

Because parents may adjust their investment in the current brood by changing the quality of their care, we also examined the effect of brood reduction on the parental care behavior of males and females. This study is unusual in that individual broods were followed through their development under field conditions. The study of Jennions & Polakow (2001) is the only one to investigate experimentally the effect of brood reduction on male mate desertion in a fish. Their work, which also focused on *A. coeruleopunctatus*, differs from the current

study in that brood reduction was to 100 young rather than to 50% of the brood, and seasonal effects on male desertion were not examined as in our study because there was no marked decline in breeding conditions. Because broods in the current study were manipulated at different times of the season when breeding conditions varied, our results have important implications for understanding the trade-off between present and future reproduction.

Methods

Study Species

Aequidens coeruleopunctatus is a monogamous, substrate-guarding, Central American cichlid (Barlow 1974; Carlisle 1981, 1985). Males and females form pairs to guard fry that become independent in 3–4 wks. However, unlike most substrate-guarders, *A. coeruleopunctatus* females lay their eggs on a dead leaf (Barlow 1974). The eggs hatch into non-swimming larvae called wrigglers 3–5 d after being laid. The parents excavate a cavity in the stream substrate, transfer the wrigglers to the cavity by mouth, and guard them. After 4–5 d, the wrigglers emerge as free-swimming fry. Many pairs stay together and guard until the fry become independent, but some males in natural streams in Panama desert their broods and thus leave the care to the females (Barlow 1974; Carlisle 1981, 1985; Vélez 1999). Even when males provide parental care, they give less care than females regardless of brood stage (Vélez 1999).

Study Site

We studied a population of *A. coeruleopunctatus* from 4 Feb. to 15 Apr. 1998 on Quebrada Juan Grande (9°8' N, 79°43' W), a shallow stream (1–5 m wide) running across Pipeline Road in the Parque Nacional Soberanía in central Panama. During the dry season, the stream became a series of 0.1–1 m deep pools connected by riffles. Water temperature varied between 24 and 27°C. Pools also differed in the number of *A. coeruleopunctatus* and other fish they sustained. Potential brood predators included eight piscivorous species of which only one, *Hoplias microlepis*, is known to prey on adult *A. coeruleopunctatus* (Angermeier & Karr 1983). Juvenile cichlids were major brood predators (Vélez & Jennions, pers. obs.).

Marking Methods

We caught adult females at night using a flashlight and a hand-held dip-net. We measured their standard length to the nearest 0.1 mm using dial calipers and individually marked fish by clipping small sections of the dorsal and anal fins. Females were then released at the same location. Males were not marked because at night they separated from the brood and could not be found and during the day they were too active and capture would have been destructive to their habitat.

Brood Reduction Protocol

We monitored fish breeding activities daily along a 2-km stretch of the stream. Whenever we encountered a brood at the wriggler stage, we noted its location and the identity of the female. That evening, we subjected the brood either to an experimental treatment in which brood size was reduced ($n = 15$) or to a control treatment in which brood size was left unchanged ($n = 12$). Treatments were performed at night to minimize the stress on the fish and to avoid attracting brood predators. Each brood was randomly assigned to a treatment, except when it was the second brood in a pool in which case it was assigned to the opposite treatment. We reduced brood size by inserting a plastic tube (1 cm diameter) into the cavity containing the wrigglers and suctioning out approximately half of the brood. The mean (\pm SE) number of removed wrigglers was 110 (± 14), with a range from 50 to 245. The control broods received a sham treatment by inserting the plastic tube into the cavity and swirling it around to simulate the disturbance of the brood reduction. The age of each brood at the time of the manipulation was estimated by subtracting the number of days that it took the wrigglers to become free-swimming fry from eight (the mean number of days that it takes for a brood to develop from eggs to free-swimming fry; Vélez, unpubl. data).

We then visited each brood daily until no fry were left in the brood or the brood became independent. During these daily visits, we observed each brood for 30 min to determine whether the male was providing parental care. A male was defined as having deserted when he was not sighted with the brood. In all 27 cases, once a male left, he did not reappear on subsequent days. The duration of male care was defined as the number of days between the brood manipulation and male desertion. Because males were not marked for individual recognition, their fate after desertion could not be determined. It was not possible to determine whether females stopped providing parental care because they abandoned the broods or because the broods succumbed to predation.

Behavioral Observations

We observed parental care behavior of males and females 1 d prior to the brood manipulation. A 15-min focal observation from the bank was conducted on each parent simultaneously using binoculars and a stopwatch. We recorded and summed across the 15-min period: (i) time spent within 25 cm of the brood; (ii) number of attacks directed at brood predators (parent swam towards intruder, intruder retreated, and parent chased intruder away from the brood), including conspecific adults, conspecific juveniles, *Cichlasoma panamense*, and noncichlid fish (primarily *Astyanax* or *Brycoamericanus*); (iii) number of bites at the substrate (assumed to be feeding); and (iv) number of times males courted females other than their mates (male swam parallel to the female quivering his body laterally). After the brood manipulation, we conducted a similar 15-min focal observation on each brood during the first 2 d that the wrigglers became free-swimming fry.

Parents were observed at this stage because males in most biparental cichlids become more involved in parental care when the young have become fully mobile fry (see Keenleyside 1991 for review).

Data Analysis

We quantified the relationships between the duration of male care and female size or the date when male parental care ended using Pearson correlations. These tests were performed separately for each treatment group. In the correlation test between the duration of male care and female size in the control group, one brood had to be excluded because the female was not measured.

We also determined whether brood reduction affected the quality of male and female parental care by comparing the behavior of parents in the control and experimental groups after the brood manipulation. Because pairs were observed twice, we calculated for each parent an average for each behavioral variable and compared those averages between the two treatments. One brood had to be excluded from the control group and two broods from the experimental group, in the following analyses: comparing the time males spent with their brood; the number of times males bit at the substrate; and the number of times males courted other females. This was because males took the broods to areas (i.e. below overhanging roots) where their behavior could not be observed.

Data were analyzed using SYSTAT 6.0 (Wilkinson 1997). In all analyses, each treatment replicate constituted one data point. All tests were two-tailed unless otherwise stated, and statistical results were considered significant at an α level of 0.05. Data are presented as means \pm SE. Non-parametric statistics were used to analyze the behavioral data when they were not normally distributed.

Results

Male Desertion

Males with reduced broods stopped providing parental care significantly earlier, at 16 (\pm 2.1) d, than males with control broods, at 23 (\pm 1.8) d (Fig. 1; $t = 2.560$, $df = 25$, $p = 0.017$). The duration of male care was not significantly correlated with female size for either treatment group (control: $n = 11$, $r = -0.480$, $p = 0.135$; reduced: $n = 15$, $r = -0.210$, $p = 0.453$). The duration of male care increased across the season for males with reduced broods (Fig. 2; $n = 15$, $r = 0.736$, $p = 0.002$), but not for males with control broods ($n = 12$, $r = 0.142$, $p = 0.659$). For males in the experimental group, the number of wrigglers removed was not correlated with the duration of male care ($n = 15$, $r = 0.352$, $p = 0.198$).

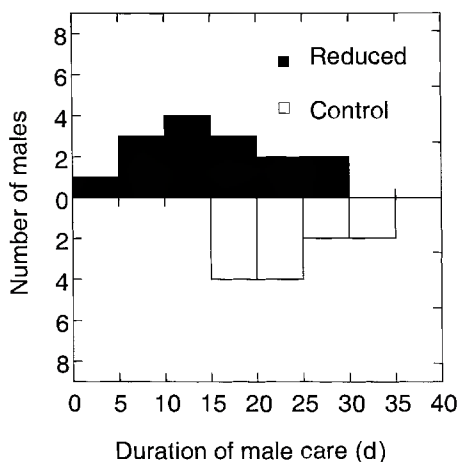


Fig. 1: Frequency distributions of the duration of male brood care for males in the control ($n = 12$) and experimental brood-reduced ($n = 15$) groups

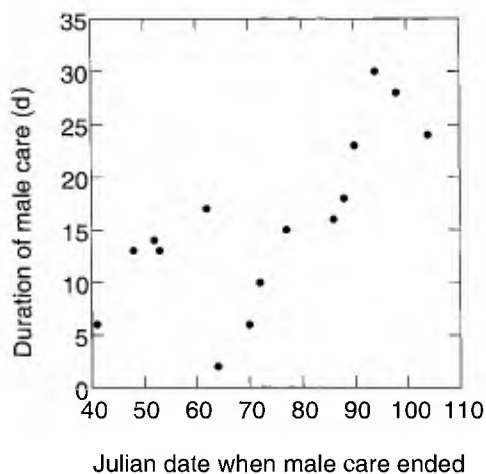


Fig. 2: Relationship between time of season (Julian date) and the duration of male care for individual groups in the experimental group ($n = 15$)

Parental Care

After the brood manipulation, males with reduced broods did not differ from males with control broods in the following: time they spent with the brood ($n_{\text{con}} = 12$, $n_{\text{exp}} = 15$, Mann-Whitney $U = 118.5$, $p = 0.163$); the number of attacks directed at potential predators ($n_{\text{con}} = 11$, $n_{\text{exp}} = 13$, $U = 87.0$, $p = 0.362$); the number of bites at the substrate ($n_{\text{con}} = 11$, $n_{\text{exp}} = 13$, $U = 55.5$, $p = 0.339$); or the number of times they courted females other than their mates

($n_{\text{con}} = 11$, $n_{\text{exp}} = 13$, $U = 86.5$, $p = 0.181$). Prior to the brood manipulation, control and experimental males did not differ in any measure of behavior.

Similarly, after the brood manipulation, females with reduced broods did not differ from females with control broods in the following: time they spent with the brood ($n_{\text{con}} = 12$, $n_{\text{exp}} = 15$, Mann-Whitney $U = 88.5$, $p = 0.906$); the number of attacks directed at potential predators ($n_{\text{con}} = 12$, $n_{\text{exp}} = 15$, $U = 103.0$, $p = 0.525$); or the number of bites at the substrate ($n_{\text{con}} = 12$, $n_{\text{exp}} = 15$, $U = 118.5$, $p = 0.161$). Prior to the brood manipulation, experimental and control females did not differ in any measure of behavior, nor in standard length or brood age at the time of manipulation.

Discussion

Male Desertion

Aequidens coeruleopunctatus males with experimentally reduced broods stopped providing parental care earlier than males whose broods were not reduced. This finding is consistent with the model developed by Lazarus (1990), which predicts that males should desert when $V_1 + M > V_2$. A reduction in brood size would have lowered both V_1 (number of surviving young with female care only) and V_2 (number of surviving young with biparental care) relative to M (expected increment in male reproductive success by deserting). If M varied randomly with respect to the treatment groups, then males with reduced broods may have stopped providing care earlier because the expected benefits from providing care for the current brood were lower than the opportunity costs or the missed opportunities to breed (Wisenden 1994). This interpretation is supported by Jennions & Polakow (2001). In their study, *A. coeruleopunctatus* males with broods reduced to 100 young deserted sooner than males with sham-treated broods.

While many experimental studies on fish have examined the relationship between brood size and the intensity of parental care (Sargent 1997), few have investigated the effect of brood size on the duration of care (Jennions & Polakow 2001). This is in sharp contrast to experimental studies on birds (e.g. Beissinger 1990; Winkler 1991), which provide support for the hypothesis that brood reduction promotes mate desertion because the benefits of desertion increase relative to the gains from providing further care.

In our study, males with reduced broods stayed longer with their broods as the season progressed. This result is consistent with Lazarus's (1990) model. Breeding conditions affect M , or the increment in male reproductive success from deserting. When breeding conditions deteriorate, the probability that the male will breed again and successfully rear a brood to independence decreases. Under such conditions, the benefits of deserting are lowered relative to the gains of providing continued care. Therefore, if late in the season breeding conditions deteriorate, then males should stay longer with broods laid late in the season. Support for this interpretation comes from the decline in breeding attempts with

season. In the first month of this study, 10 new broods were started. This number increased to 16 in the second month and decreased to one in the last month. This sharp decline in breeding attempts late in the season was accompanied by receding water levels as the dry season advanced, which deteriorated breeding conditions. The small number of breeding attempts late in the season was not due to a lack of unmated individuals because we found many unmated adults in the stream during our daily censuses. Broods initiated near the end of the breeding season at a second Panamanian study site were more likely to fail (Jennions et al., unpubl. data).

If breeding conditions deteriorated late in the season, then why did males with control broods not increase the duration of care late in the season? The mate desertion model of Lazarus (1990) predicts that males should desert when $V_1 + M$ exceeds V_2 . Because brood reduction lowered V_1 for experimental males but not for control males, it is possible that the V_1 of control males was high enough late in the season so that $V_1 + M$ exceeded V_2 even when M was low. Brood reduction may have lowered the V_1 of experimental males to a level where $V_1 + M$ no longer exceeded V_2 .

Parental Care

Several studies on fishes, birds and mammals (see Clutton-Brock 1991 for review) have shown that parental care effort increases with brood size. In *A. coeruleopunctatus*, males and females with reduced broods did not provide less care per day than those with control broods. While these results may indicate that the sexes value present and future reproduction similarly, the shorter duration of care by males with reduced broods vs. males with control broods suggests that males trade off present and future reproduction differently from females. Our results suggest that males invest in parental care according to the value of the brood, not by adjusting the quality of care but rather the period over which they provide this care. In contrast, females in this study never abandoned their broods before their mates did and always continued to provide parental care after their mates deserted.

Jennions & Polakow (2001) found that reducing brood size to 100 in *A. coeruleopunctatus* pairs decreased male defence and male time with the brood but did not affect female parental care. However, if the number of attacks was adjusted for the time that males spent away from the brood, then brood reduction had no effect on male defence. Jennions & Polakow (2001) also attributed the decline in male time with the brood to males temporarily leaving the brood to engage in extra-pair courtship. The 20% of males that deserted and immediately re-mated appeared to spend more time courting extra-pair females than did other males. This result is consistent with our interpretation that males trade off present and future reproduction by adjusting the duration and not the quality of parental care when present with the brood.

Previous studies on the trade-off between present and future reproduction have examined how much care parents provide at a particular stage in the

development of the brood and/or at a specific time in the season (see Sargent 1997 for review). By following individual broods through their development at different times of the season, we have shown that the single-stage, single-time approach may be misleading. First, if we had compared the parental care behavior of parents with control and reduced broods without following broods to determine when males deserted, we might have concluded that males and females both show no response to a reduction in brood size. However, because individual broods were followed through their development, we discovered that males adjust their investment in present reproduction by changing the duration of care. Secondly, by observing broods laid at different times of the season, we learned that male care behavior varied with breeding opportunities. Early in the season, the payoff from desertion was higher than late in the season when breeding conditions deteriorated. To understand fully the variation in parental care patterns in animals, future studies should identify the factors that affect both the quality and duration of parental care, and how their effects change over time.

Acknowledgements

We thank H. Jane Brockmann and Laura Sirot for their comments on this manuscript. We are also grateful to Pat Backwell and John Christy for their support while conducting this research. This study was funded by grants from the University of Florida and Sigma Xi Society to MJV, and by a grant from the Smithsonian Tropical Research Institute to MDJ.

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Received: April 10, 2001

Initial acceptance: August 3, 2001

Final acceptance: September 26, 2001 (J.-G. Godin)